Mike Service



MEDICAL ENTOMOLOGY for Students

FIFTH EDITION



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Medical Entomology for Students

FIFTH EDITION

Despite numerous scientific investigations on vector-borne human infections such as malaria, filariasis, Lyme disease and typhus, these diseases continue to threaten human health. Understanding the role of vectors in disease transmission, and the most appropriate control strategies, is therefore essential. This book provides information on the recognition, biology, ecology and medical importance of the arthropods that affect human health.

The fifth edition of this popular textbook is completely updated, incorporating the latest strategies for controlling insects, ticks and mites. Numerous illustrations, with new colour photographs of some of the most important vectors, aid recognition. A glossary of entomological and epidemiological terms is included, along with a list of commonly used insecticides and their trade names.

Clearly presented in a concise style, this text is aimed at students of medical entomology, tropical medicine, parasitology and pest control. It is also essential reading for physicians, health officials and community health workers.

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Fifth Edition

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To Wendy, for all her help over many years with this and previous publications

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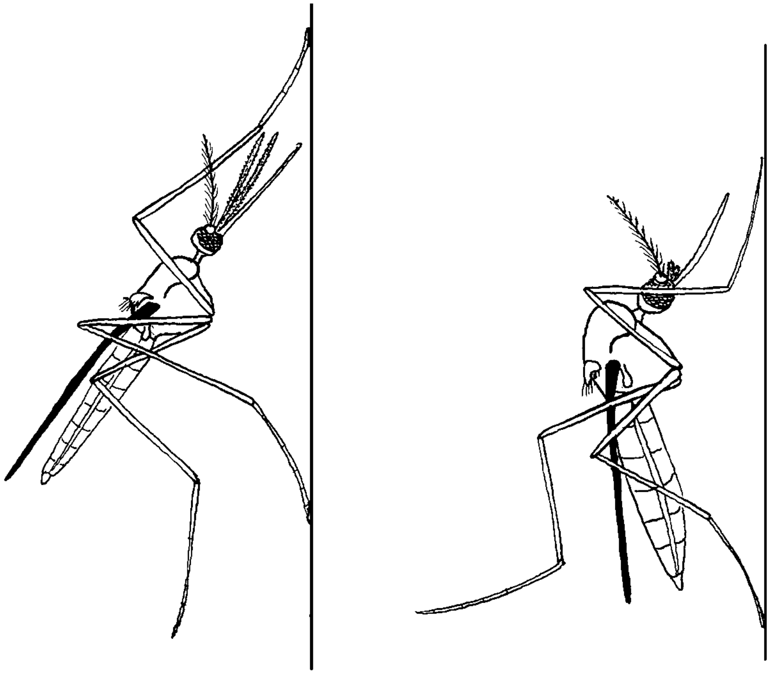
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1

Introduction to mosquitoes (Culicidae)



There are some 3530 species of mosquitoes, which are traditionally placed in 43 genera, all contained in the family Culicidae. However, some mosquito experts recognize a different classification that has many more (113) genera. For example, some mosquitoes previously in the genus *Aedes* have been transferred to genera such as *Ochlerotatus* and *Stegomyia*. This results in *Aedes albopictus* and *Aedes aegypti* becoming *Ochlerotatus albopictus* and *Stegomyia aegypti*. However, as these new names are not so well known to non-mosquito experts I have retained the older names such as *Aedes albopictus* and *Aedes aegypti*.

Mosquitoes are divided into three subfamilies: Toxorhynchitinae, Anophelinae (anophelines) and Culicinae (culicines). Mosquitoes have a worldwide distribution, occurring throughout the tropical and temperate regions and northwards into the Arctic Circle. The only areas from which they are absent are Antarctica and a few islands. They have been found at elevations of 3500 m and down mines to depths of 1250 m below sea level.

The most important pest and vector species belong to the genera *Anopheles*, *Culex*, *Aedes*, *Psorophora*, *Mansonia*, *Haemagogus* and *Sabethes*. *Anopheles* species, as well as transmitting malaria, are vectors of filariasis (*Wuchereria bancrofti*, *Brugia malayi* and *Brugia timori*) and a few arboviruses. Some *Culex* species also transmit *Wuchereria bancrofti* as well as several arboviruses. *Aedes* species are important vectors of yellow fever, dengue, West Nile virus and many other arboviruses, and in a few restricted areas they also transmit *Wuchereria bancrofti* and *Brugia malayi*. *Mansonia* species transmit *Brugia malayi* and sometimes *Wuchereria bancrofti* and a few arboviruses. *Haemagogus* and *Sabethes* mosquitoes are vectors of yellow fever and a few other arboviruses in Central and South America, while the genus *Psorophora* contains a few species that transmit arboviruses and others that are troublesome biters in North and South America.

Many mosquitoes which are not vectors can nevertheless be troublesome because of the serious biting nuisances they cause.

1.1 External morphology

Mosquitoes possess only one pair of functional wings, the fore-wings. The hind-wings are represented by a pair of small, knob-like halteres. Mosquitoes are distinguished from other flies of a somewhat similar shape and size by: (1) the possession of a conspicuous forward-projecting proboscis; (2) the presence of numerous appressed scales on the thorax, legs, abdomen and wing veins; and (3) a fringe of scales along the posterior margin of the wings.

Mosquitoes are slender and relatively small insects, usually measuring about 3–6 mm in length. Some species, however, can be as small as 2 mm while others may be as long as 19 mm. The body is distinctly divided into a head, thorax and abdomen.

The head has a conspicuous pair of kidney-shaped compound eyes. Between the eyes arises a pair of filamentous and segmented antennae. In females the antennae have whorls of short hairs (i.e. pilose antennae), but in males, with a few exceptions in genera of no medical importance, the antennae have many long hairs giving them a feathery or plumose appearance. Mosquitoes can thus be conveniently sexed by examination of their ***antennae***: individuals with feathery antennae are males, while those with only short and rather inconspicuous antennal hairs are females (Figs. 1.1, 1.13). Just below the antennae is a pair of ***palps***, which in female anophelines are pointed apically while in males they are dilated. In female culicines the palps are very short while in males they are long (Fig. 1.13). Arising between the palps is the single long ***proboscis***, which in females contains the piercing mouthparts. In mosquitoes the proboscis characteristically projects forwards (Fig. 1.1).

The thorax is covered, dorsally and laterally, with scales, which may be dull or shiny, white, brown, black or almost any colour. It is the arrangement of black and white, or coloured, scales on the dorsal surface of the thorax that gives many species, especially *Aedes* mosquitoes, their distinctive patterns (Fig. 3.3).

The wings are long and relatively narrow, and the number and arrangement of the wing veins is virtually the same for all mosquito species (Fig. 1.1). The veins are covered with scales which are usually brown, black, white or yellowish, but more brightly coloured scales may occasionally be present. The shape of the scales and the pattern they create differs considerably between both genera and species of mosquitoes. Scales also project as a fringe along the posterior border of the wings. In life the wings of resting mosquitoes are placed across each other over the abdomen in the fashion of a closed pair of scissors. The legs are long and slender and are covered with scales which are usually brown, black or white and may be arranged in patterns, often in the form of rings (Fig. 3.4b). The tarsus usually terminates in a pair of toothed or simple claws. Some genera, such as *Culex*, have a pair of small fleshy pulvilli (Fig. 1.2) between the claws in addition to the empodium.

The abdomen is composed of 10 segments, but only the first seven or eight are visible. Mosquitoes in the subfamily Culicinae usually have the abdomen covered dorsally and ventrally with mostly brown, blackish or whitish scales. In the Anophelinae, however, the abdomen is almost, or entirely, devoid of scales. The last abdominal segment of a female mosquito terminates in a pair of small finger-like cerci, whereas in males there is a pair of prominent claspers, comprising part of the male external genitalia.

In unfed mosquitoes the abdomen is thin and slender, but after females have bitten a host and taken a blood-meal (only females bite) the abdomen becomes greatly distended and resembles an oval red balloon. When the abdomen is full of developing eggs it is also dilated, but whitish and not red in appearance.

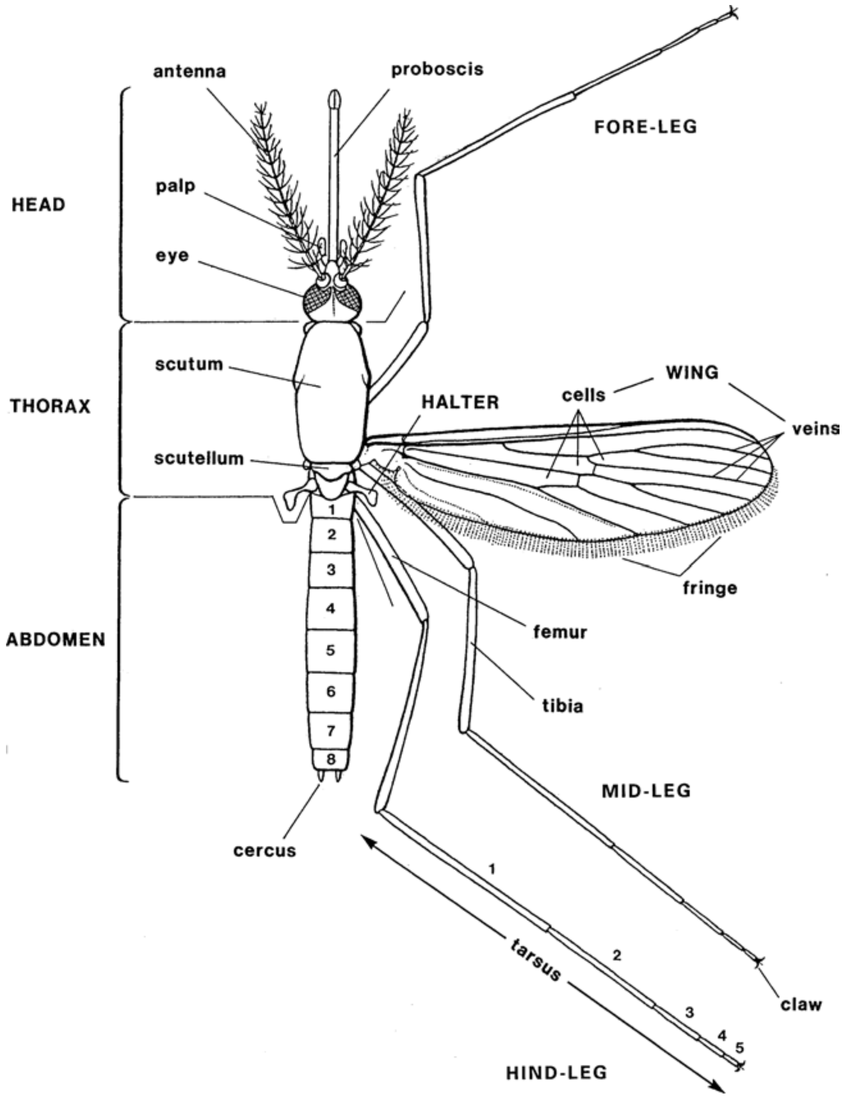


Figure 1.1 Diagrammatic representation of a female adult mosquito.

1.1.1 Mouthparts and salivary glands

The mouthparts are collectively known as the ***proboscis***. In mosquitoes the proboscis is long and projects conspicuously forwards in both sexes – although males do not bite. The largest component of the mouthparts is the long and flexible gutter-shaped labium, which terminates in a pair of small flap-like structures called labella. In cross-section the labium is seen to almost encircle all other components of the mouthparts (Fig. 1.3), and it serves as a protective sheath. The individual components are held close

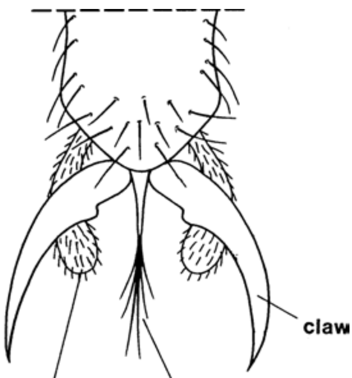


Figure 1.2 Tip of the last segment of the tarsus of a *Culex* mosquito showing claws, hair-like empodium and two large pulvilli.

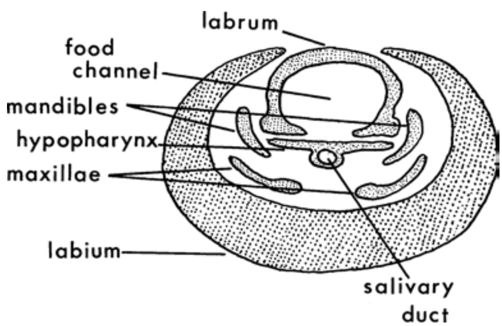


Figure 1.3 Diagram of a cross-section through the proboscis of a mosquito, showing components of the mouthparts and food channel.

together in life and only become partially separated during blood-feeding, or when they are teased apart for examination as illustrated in Figure 1.4.

The uppermost structure, the labrum, is slender, pointed and grooved along its ventral surface. In between this 'upper roof' (labrum) and 'lower gutter' (labium) are five needle-like structures, namely a lower pair of toothed maxillae, an upper pair of mandibles, which usually lack teeth (although in *Anopheles* they are very finely toothed), and finally a single untoothed hollow stylet called the hypopharynx. When a female mosquito bites a host the labella, at the tip of the fleshy labium, are placed on the skin and the labium, which cannot pierce the skin, curves backwards. This allows the paired mandibles, paired maxillae, labrum and hypopharynx to penetrate the host's skin. Saliva from a pair of trilobed salivary glands (Fig. 1.14), situated ventrally in the anterior part of the thorax, is pumped

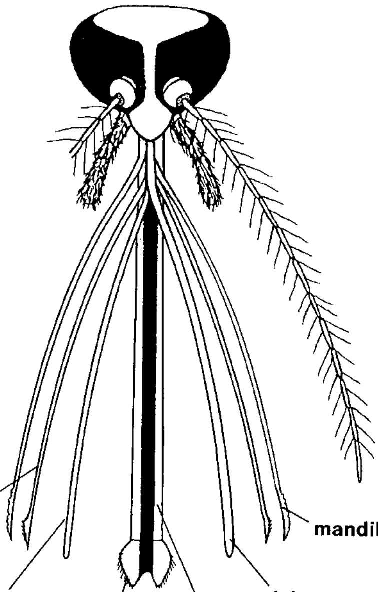


Figure 1.4 Diagram of the head of a female culicine mosquito, showing the components of the mouthparts spread out from the labium.

down the hypopharynx. ***Saliva*** contains antihaemostatic enzymes that produce haematomas in the skin and facilitate the uptake of blood. Saliva also contains anticoagulants to prevent blood from clotting and obstructing the mouthparts as it is sucked up, and anaesthetic substances that help reduce the pain inflicted by the mosquito's bite, so reducing the host's defensive reactions.

Although male mosquitoes have a proboscis, the maxillae and mandibles are usually reduced in size or the mandibles are absent, and consequently males cannot bite.

1.2 Life cycle

1.2.1 Blood-feeding and the gonotrophic cycle

Most mosquitoes mate shortly after emergence from the pupa. Sperm from a male enter the spermotheca of a female, and this usually serves to fertilize all eggs laid during her lifetime; thus only one mating and insemination per female is required. With a few exceptions, a female mosquito must bite a host and take a blood-meal to obtain the necessary nutrients for the development of her eggs. This is the normal procedure and is referred to as ***anautogenous*** development. A few species, however, can develop the first

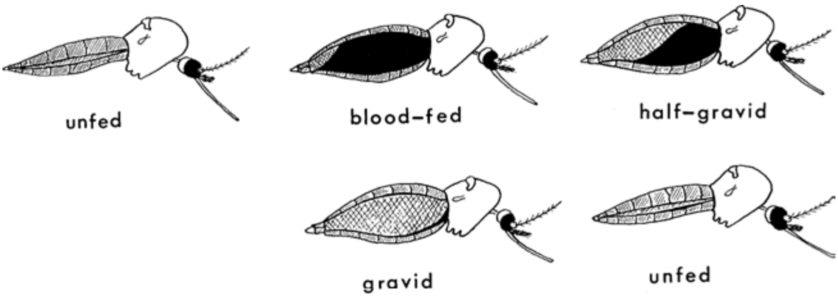


Figure 1.5 Diagrammatic representation of the gonotrophic cycle of a female mosquito. Each cycle begins with an unfed adult, which passes through a blood-fed, half-gravid and gravid condition. After oviposition the female is again unfed and seeks another blood-meal.

batch of eggs without a blood-meal, and more rarely subsequent batches. This process is called *autogenous* development. The speed of digestion of the blood-meal depends on temperature. In most tropical species it takes only 2–3 days, but in colder, temperate countries blood digestion often takes as long as 7–14 days.

After a blood-meal the mosquito's abdomen is dilated and bright red, but some hours later the abdomen becomes a much darker red. As the blood is digested and the white eggs in the ovaries enlarge, the abdomen becomes whitish posteriorly and dark reddish anteriorly. This condition represents a mid-point in blood digestion and ovarian development, and the mosquito is referred to as being half-gravid (Fig. 1.5). Eventually all blood is digested and the abdomen becomes dilated and whitish due to the formation of fully developed eggs (Fig. 1.5). The female is now said to be gravid, and she searches for suitable larval habitats in which to lay her eggs. After oviposition the female mosquito takes another blood-meal, and after 2–3 days (in the tropics) a further batch of eggs is matured and laid. This process of blood-feeding and egg-laying is repeated several times throughout the female's life and is referred to as the *gonotrophic cycle*.

Male mosquitoes cannot bite but feed on the nectar of flowers and other naturally occurring sugary secretions. Males are consequently unable to transmit any diseases. Sugar-feeding is not, however, restricted to males: females may also feed on sugary substances to obtain energy for flight and dispersal, but only in a few species (the autogenous ones) is this type of food sufficient for egg development.

1.2.2 Oviposition and biology of the eggs

Depending on the species, female mosquitoes lay about 30–300 eggs in one oviposition. Eggs are brown or blackish and 1 mm or less in length. In many Culicinae they are elongate or approximately ovoid in shape, but eggs of

Mansonia are drawn out into a terminal filament (Fig. 3.8). In the Anophelinae eggs are usually boat-shaped (Fig. 1.8). Many mosquitoes, such as species of *Anopheles* and *Culex*, lay their eggs directly on the water surface. In *Anopheles* the eggs are laid singly and float on the water, whereas *Culex* eggs are laid vertically in several rows held together by surface tension to form an ***egg raft*** which floats on the water (Fig. 1.15). *Mansonia* species lay their eggs in a sticky mass that is glued to the underside of floating plants. None of the eggs of these mosquitoes can survive desiccation, and consequently they die if they become dry. In the tropics eggs hatch within 2–3 days, but in cooler temperate countries they may not hatch until after 7–14 days, or longer.

Other mosquitoes, such as those belonging to the genera *Aedes*, *Psorophora* and *Haemagogus*, do not lay eggs on the water surface. Instead they deposit them just above the water line on damp surfaces, such as mud and leaf litter, or on the inside walls of tree-holes and clay water-storage pots. Eggs of these genera can withstand desiccation, especially those of *Aedes* and *Psorophora*, which can remain dry for months or even years but still remain viable and hatch when covered with water. Because their eggs are laid above the water line of larval habitats it may be many weeks or months before they become flooded with water and can hatch. However, even when flooded, hatching may extend over relatively long periods because the eggs hatch in instalments. Moreover, eggs of *Aedes* and *Psorophora* may require repeated immersions in water followed by short periods of desiccation before they will hatch. *Aedes* and *Psorophora* eggs may also enter a state of ***diapause***, that is not hatching until some specific environmental stimulus such as a change in day length and/or temperature breaks diapause and the eggs hatch. In temperate regions many *Aedes* and *Psorophora* species overwinter as diapausing eggs.

1.2.3 Larval biology

Mosquito larvae are distinguished from most other aquatic insects by being legless and having an enlarged thorax that is wider than both the head and the abdomen. There are four active larval ***instars***. All mosquito larvae require water in which to develop; no mosquito has larvae that can withstand desiccation, although they may be able to survive short periods, for example, in wet mud.

Larvae have a well-developed head bearing a pair of antennae and a pair of compound eyes. Prominent mouthbrushes are present in most species and serve to sweep water containing minute food particles into the mouth. The thorax is roundish and has unbranched and branched hairs, which are usually long and conspicuous. The 10-segmented abdomen has nine visible segments, most of which have unbranched or branched hairs (Figs. 1.9, 1.16). The last segment, which differs in shape from the preceding eight

segments, has two paired groups of long hairs forming the caudal setae, and a larger fan-like group comprising the ***ventral brush*** (Figs. 1.10, 1.16). This last segment ends in two pairs of transparent sausage-shaped anal papillae, which although often called gills are concerned not with respiration but with osmoregulation.

Mosquito larvae, with the exception of *Mansonia* and *Coquillettidia* species (and a few other species), must come to the water surface to breathe. Atmospheric air is taken in through a pair of spiracles situated dorsally on the ninth abdominal segment. In the subfamilies Toxorhynchitinae and Culicinae these spiracles are situated at the end of a single dark-coloured and heavily sclerotized tube termed the ***siphon*** (Fig. 1.16). *Mansonia* and *Coquillettidia* larvae possess a specialized siphon that is more or less conical, pointed at the tip and supplied with prehensile hairs and serrated cutting structures (Fig. 3.9). These enable the siphon to be inserted into the roots or stems of aquatic plants, from which oxygen for larval respiration is obtained. In contrast, larvae of the Anophelinae do not have a siphon (Figs. 1.10, 1.13).

Mosquito larvae feed on yeasts, bacteria, protozoans and numerous other microorganisms, as well as on decaying plant and animal material found in the water. Some, such as *Anopheles* species, are surface-feeders, whereas many others species browse over the bottoms of habitats. A few mosquitoes are carnivorous or cannibalistic. There are four larval instars, and in tropical countries larval development, that is the time from egg hatching to pupation, can be as short as 5–7 days, but many species require about 7–14 days. In temperate areas the larval period may last several weeks or months, and several species overwinter as larvae.

1.2.4 Larval habitats

Mosquito larval habitats vary from large and usually permanent collections of water, such as freshwater swamps, marshes, ricefields and borrow pits, to smaller collections of temporary water such as pools, puddles, water-filled car tracks and animal footprints, ditches, drains and gulleys. A great variety of 'natural container-habitats' also provide breeding places, such as water-filled tree-holes, rock-pools, bamboo stumps, bromeliads, pitcher plants, leaf axils in bananas, pineapples and other plants, water-filled split coconut husks and even snail shells. Larvae also occur in wells and 'man-made container-habitats', such as clay pots, water-storage jars, tin cans, discarded kitchen utensils and motor-vehicle tyres. Some species prefer shaded larval habitats whereas others like sunlit habitats. Many species cannot survive in water polluted with organic debris, whereas others occur in water contaminated with excreta or rotting vegetation. A few mosquitoes are found almost exclusively in brackish or salt waters, such as saltwater marshes and mangrove swamps, and are consequently restricted to mostly coastal areas.

Some species are less specific in their requirements and can tolerate a wide range of different types of larval habitats.

Almost any collection of permanent or temporary water can be a mosquito larval habitat, but larvae are usually absent from large expanses of uninterrupted water such as lakes, especially if they have large numbers of fish and other predators. They are also usually absent from large rivers and fast-flowing waters, but they may occur in marshy areas and isolated pools and puddles formed at the edges of flowing water.

1.2.5 Pupal biology

All mosquito pupae are aquatic and comma-shaped. The head and thorax are combined to form the ***cephalothorax***, which dorsally has a pair of respiratory ***trumpets*** (Fig. 1.6). The abdomen is 10-segmented, although only eight segments are visible. Each segment has numerous short hairs, and the last segment terminates in a pair of oval and flattened structures termed ***paddle***s (Figs. 1.11, 1.18). Some of the developing structures of the adult mosquito can be seen through the integument of the cephalothorax, the most conspicuous features being a pair of dark compound eyes, folded wings, legs and the proboscis (Fig. 1.6).

Pupae do not feed but spend most of their time at the water surface taking in air through the respiratory trumpets. If disturbed they swim up and down in the water in a jerky fashion.

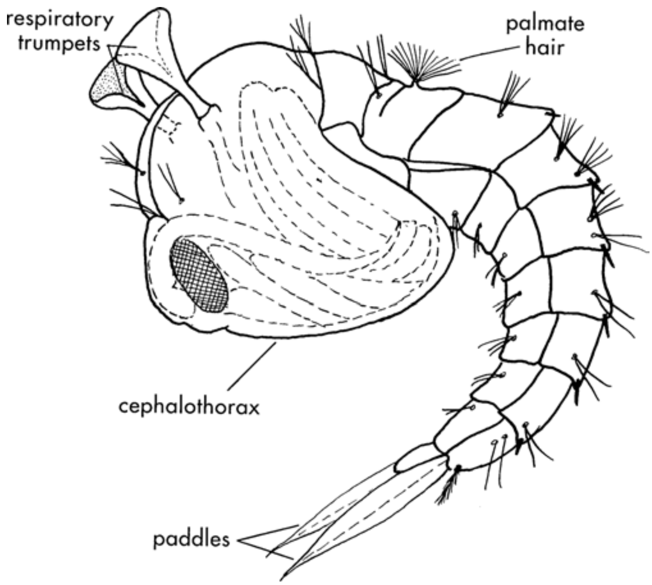


Figure 1.6 *Anopheles* pupa.

Pupae of *Mansonia* and *Coquillettidia* differ in that they have relatively long breathing trumpets, which are modified to enable them to pierce aquatic vegetation and obtain their oxygen in a similar fashion to the larvae (Fig. 3.9). As a consequence their pupae remain submerged and rarely come to the water surface.

In the tropics the pupal period lasts only 2–3 days, but in cooler temperate regions pupal development may take 9–12 days, or longer. At the end of pupal life the skin on the dorsal surface of the cephalothorax splits, and the adult mosquito struggles out.

1.2.6 Adult biology and behaviour

As already mentioned (page 6), females of most mosquito species require a blood-meal before the eggs can develop, and this is taken either before or more usually after mating. Many species bite humans to obtain their blood-meals, and a few feed on humans in preference to other animals. However, others prefer feeding on non-human hosts, and many species never bite people. Species that usually feed on humans are said to be ***anthropophagic*** in their feeding habits, whereas those feeding mainly on other animals are called ***zoophagic***. Mosquitoes that feed on birds are sometimes called ***ornithophagic*** instead of zoophagic. Females are attracted to hosts by various stimuli emanating from their breath or sweat, such as carbon dioxide, lactic acid, octenol, as well as body odours and warmth. Vision usually plays only a minor role in host orientation. Some species feed more or less indiscriminately at any time of the day or night; others are mainly diurnal or nocturnal in their biting habits.

A few species of mosquitoes frequently enter houses to feed and are said to be ***endophagic*** in their feeding habits, whereas those that bite their hosts outside houses are called ***exophagic***. After having bitten humans, or other hosts, either inside or outside houses, mosquitoes seek resting places in which to shelter during digestion of the blood-meal. Some species rest inside houses during blood digestion and development of the eggs and are called ***endophilic***. In contrast, mosquitoes that rest outdoors are termed ***exophilic***. Female adults of *Aedes aegypti* (a vector of yellow fever and dengue), for example, are usually anthropophagic, exophagic and exophilic, whereas adults of *Anopheles gambiae* (African malaria vector) are mainly anthropophagic, endophagic and endophilic. However, many species are not entirely anthropophagic or zoophagic, endophagic or exophagic, endophilic or exophilic, but show various degrees of these behavioural patterns; in other words all these terms are relative. The feeding behaviour of a species may also change. For example, in certain areas and at certain seasons a species may bite people predominantly (anthropophagic) inside houses (endophagic) and remain in houses afterwards (endophilic), but if there are few people but many animals in the area, the species may become

predominantly zoophagic, and also exophagic and exophilic. Many species are less adaptable in their feeding behaviour and will never rest in houses or enter them to feed on the occupants.

The ***biting behaviour*** of female mosquitoes may be very important in the epidemiology of disease transmission. Mosquitoes feeding on people predominantly out of doors and late at night will not bite many young children, because they will be indoors and asleep at this time. Consequently young children will be less likely to be infected with diseases that these mosquitoes might transmit. During hot and dry seasons substantial numbers of people may sleep out of doors and as a consequence be bitten more frequently by exophagic mosquitoes. Some mosquitoes bite predominantly within forests or wooded areas, so people are likely to get bitten when they visit such sites. Clearly the behaviour of both people and mosquitoes may be relevant in disease transmission.

The resting behaviour of adult mosquitoes may be important in planning control measures. In several malaria control campaigns the interior surfaces of houses, such as walls and ceilings, are sprayed with residual insecticides to kill adult mosquitoes resting on them. This approach will, of course, only be effective in controlling malaria if the mosquito vectors are endophilic (see Chapter 2, page 49).

Many mosquitoes probably disperse only a few hundred metres from their emergence sites, so in control programmes and epidemiological studies it is usually safe to say that mosquitoes will not fly further than about 2 km. There are records of mosquitoes being found 100 km or more from their larval habitats, but such dispersal is nearly always wind-assisted. Mosquitoes may get transported long distances in aeroplanes, and sometimes this causes disease outbreaks, such as 'airport malaria'.

In tropical countries adult female mosquitoes probably live ***on average*** 1–2 weeks, whereas in temperate countries adult longevity is likely to be 3–4 weeks. Species that hibernate or aestivate live much longer: for example in Europe some fertilized female *Culex pipiens* survive in hibernation from August until May. Adult males usually have a shorter life span than females.

1.3 Classification of mosquitoes

1.3.1 Subfamily Toxorhynchitinae

The Toxorhynchitinae comprise a single genus, *Toxorhynchites*, which contains about 94 species that are mainly tropical, although a few species occur in North America, southeastern Russia and Japan.

Adults are large (19 mm long, 24 mm wingspan) and colourful, being metallic bluish or greenish with black, white or red tufts of hair-like scales projecting from the posterior abdominal segments. Adults are easily

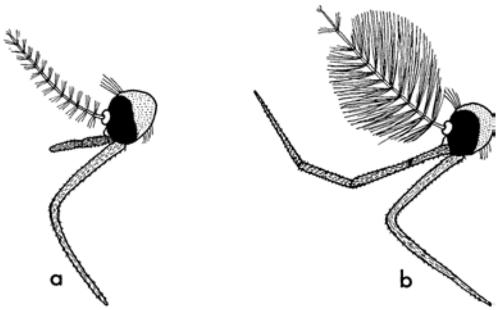


Figure 1.7 Heads of *Toxorhynchites* adults: (a) female; (b) male.

recognized by having a proboscis that is curved backwards in both sexes (Fig. 1.7) and that is incapable of piercing the skin. Consequently, since neither sex can bite, they are of no medical importance. Their larvae are also large (12–18 mm long), often dark reddish and, like those of the Culicinae, have a siphon. They are predaceous on larvae of other mosquitoes and on their own kind. They have occasionally been introduced into areas in the hope that their voracious larvae will help reduce the numbers of pest mosquitoes. Larvae are found mainly in container-habitats, such as tree-holes and bamboo stumps, tin cans and water-storage pots.

1.3.2 Subfamily Anophelinae

Of the three genera included in the subfamily Anophelinae only the genus *Anopheles* (about 477 species) is medically important, for instance as malaria vectors. The following characters serve to separate anopheline from culicine mosquitoes.

Anopheline eggs

Eggs are laid singly on the water surface. In most species they are typically boat-shaped, and laterally have a pair of air-filled sacs called ***floats*** (Fig. 1.8). Anopheline eggs are unable to withstand desiccation.

Anopheline larvae

Larvae lack a siphon and lie ***parallel*** to the water surface, not subtended at an angle as are the culicines. They are surface-feeders and so spend most of their time at the water surface. Examination under a microscope shows that the abdomen has small, brown, sclerotized plates, called ***tergal plates***, on the dorsal surface of abdominal segments 1–8; there may also be 1–3 small accessory plates behind a main tergal plate. In addition, most or all of these segments have a pair of well-developed ***palmate hairs***, sometimes called float hairs (Figs. 1.1, 1.9). These abdominal palmate hairs and a single pair

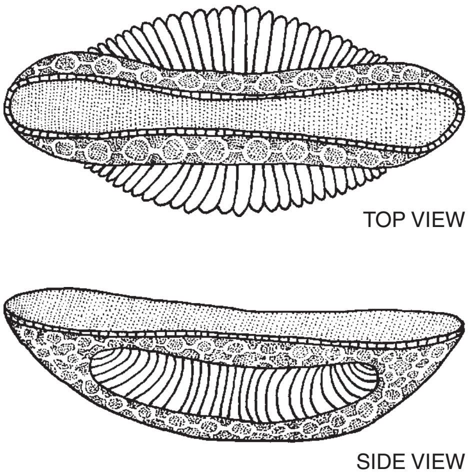


Figure 1.8 *Anopheles* eggs.

on the thorax come into contact with the water surface and aid in keeping larvae parallel to the surface. Laterally on each side of segment 8 (8 and 9 are combined) there is a sclerotized comb-like structure with teeth called the ***pecten***. All these structures identify larvae as belonging to the genus *Anopheles*.

Anopheline pupae

The respiratory trumpets of anopheline pupae are short and broad distally, thus appearing conical (Figs. 1.6, 1.11a), whereas in most culicines the trumpets are narrower and more cylindrical. The most reliable character for identifying anopheline pupae is the presence of short, peg-like spines situated laterally near the distal margins of abdominal segments 2–7 or 3–7 (Fig. 1.11b); in culicines there are no such spines.

Anopheline adults

Adult *Anopheles* usually rest with their bodies at an ***angle*** to the surface, that is with the proboscis and abdomen in a straight line, or 'head down bottom up' (Fig. 1.13, Plate 1). In some species they rest at almost right angles to the surface, whereas in others such as the Indian mosquito *Anopheles culicifacies* the angle is much smaller. This is a very useful character, allowing adults resting in houses and elsewhere to be readily identified as *Anopheles*.

Most, but not all, *Anopheles* mosquitoes have the dark (usually black) and pale (usually white or yellowish) scales on the wing veins arranged in '***blocks***' or specific areas (Fig. 1.12) forming a distinctive spotted pattern which differs according to species. A few species, however, such as the

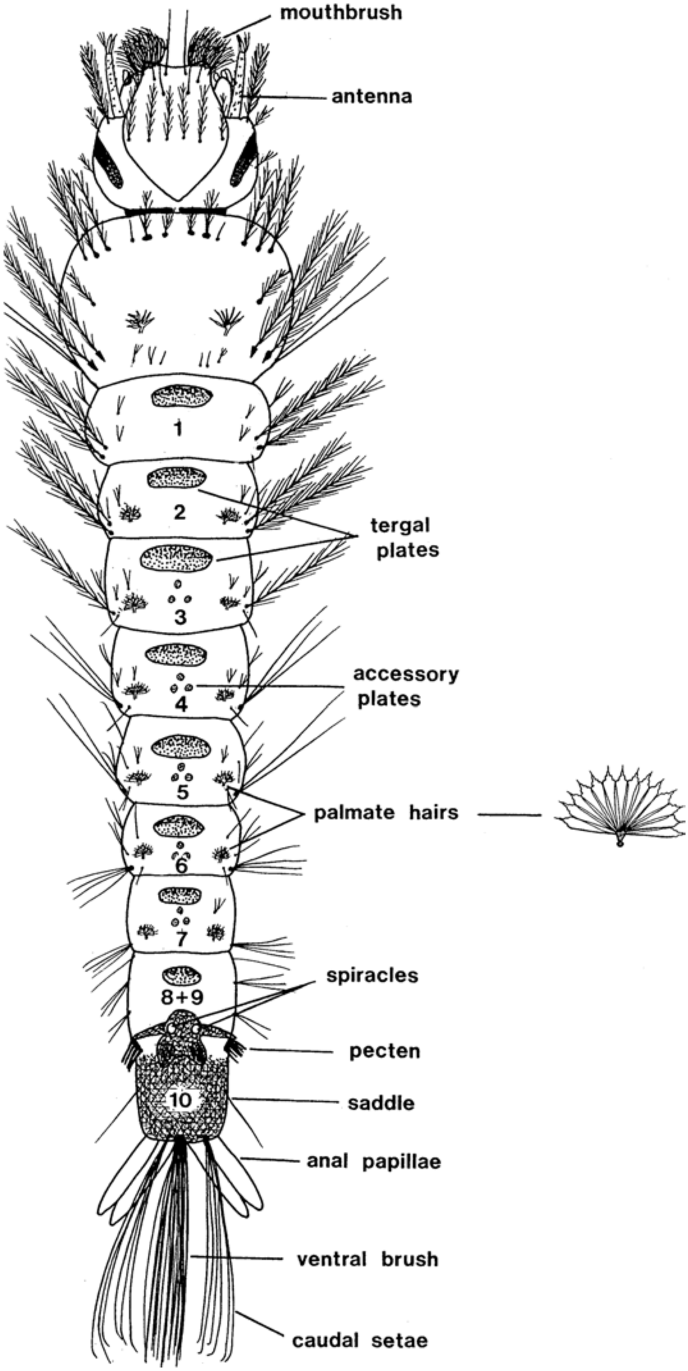


Figure 1.9 *Anopheles* larva, dorsal view, showing diagnostic abdominal tergal plates and palmate hairs.

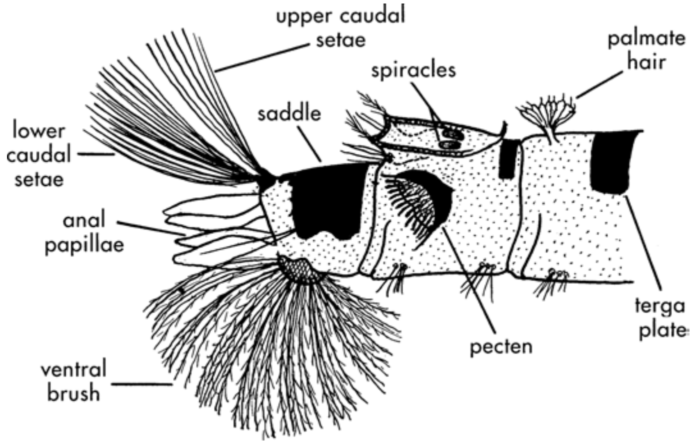


Figure 1.10 Lateral view of the abdominal terminal segments of an *Anopheles* larva.

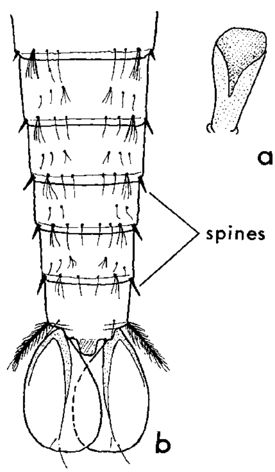


Figure 1.11 *Anopheles* pupa: (a) short and broad respiratory trumpet; (b) part of abdomen showing diagnostic spines.

European *Anopheles claviger*, have the veins covered more or less uniformly with dark (often brown) scales. The most reliable way to distinguish between adult *Anopheles* and Culicinae is by examination of their ***heads***. The first procedure is to determine the sex of the adults: female mosquitoes have non-plumose antennae whereas males have plumose antennae. If the adults are females and also *Anopheles* then the ***palps*** will be about as long as the proboscis and usually lie closely alongside it (Fig. 1.13). The palps are usually blackish with broad or narrow rings of pale scales, especially on the

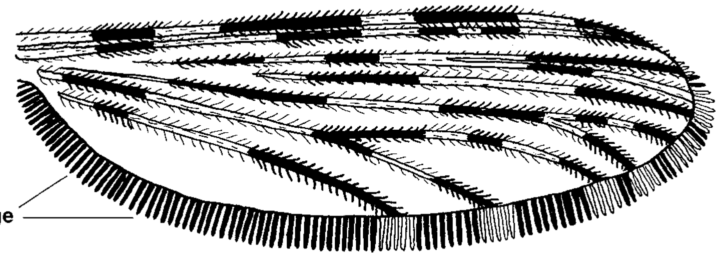


Figure 1.12 *Anopheles* wing, showing dark and pale scales arranged in 'blocks'.

apical half. In male *Anopheles* the ***palps*** are also about as long as the proboscis but are distinctly swollen at their ends and are said to be clubbed (Fig. 1.13); they may also have rings of pale scales apically.

Other differences are that in *Anopheles* there is only a single spermotheca in females, and in both sexes the middle lobe of the salivary glands is considerably shorter than the two outer lobes (Fig. 1.14).

Principal characters for separating the various stages in the life cycles of anopheline and culicine mosquitoes are given in Table 1.1.

1.3.3 Subfamily Culicinae

There are some 3053 species in the large subfamily Culicinae (belonging to 38 or 110 genera, depending on the classification used). The most important medically are the genera *Aedes*, *Culex*, *Mansonia*, *Haemagogus*, *Sabethes* and *Psorophora*. The following characters separate the Culicinae from *Anopheles* mosquitoes. Methods for distinguishing the more important genera within the Culicinae are given in Chapter 3.

Culicine eggs

Culicine eggs never have floats. They are laid either as a number of single eggs (e.g. *Aedes*) or in the form of ***egg rafts*** that float on the water surface (e.g. *Culex* and *Coquillettidia*), or are deposited as sticky masses glued to the underside of floating vegetation (e.g. *Mansonia*) (Fig. 1.15).

Culicine larvae

All culicine larvae possess a ***siphon*** (Fig. 1.16), which may be long or short. They hang upside down at an angle from the water surface when they are getting air (Fig. 1.13), except for *Mansonia* and *Coquillettidia* larvae, which insert their specialized siphons into aquatic plants and remain submerged (Fig. 3.9). There are no abdominal palmate hairs or tergal plates on culicine larvae.

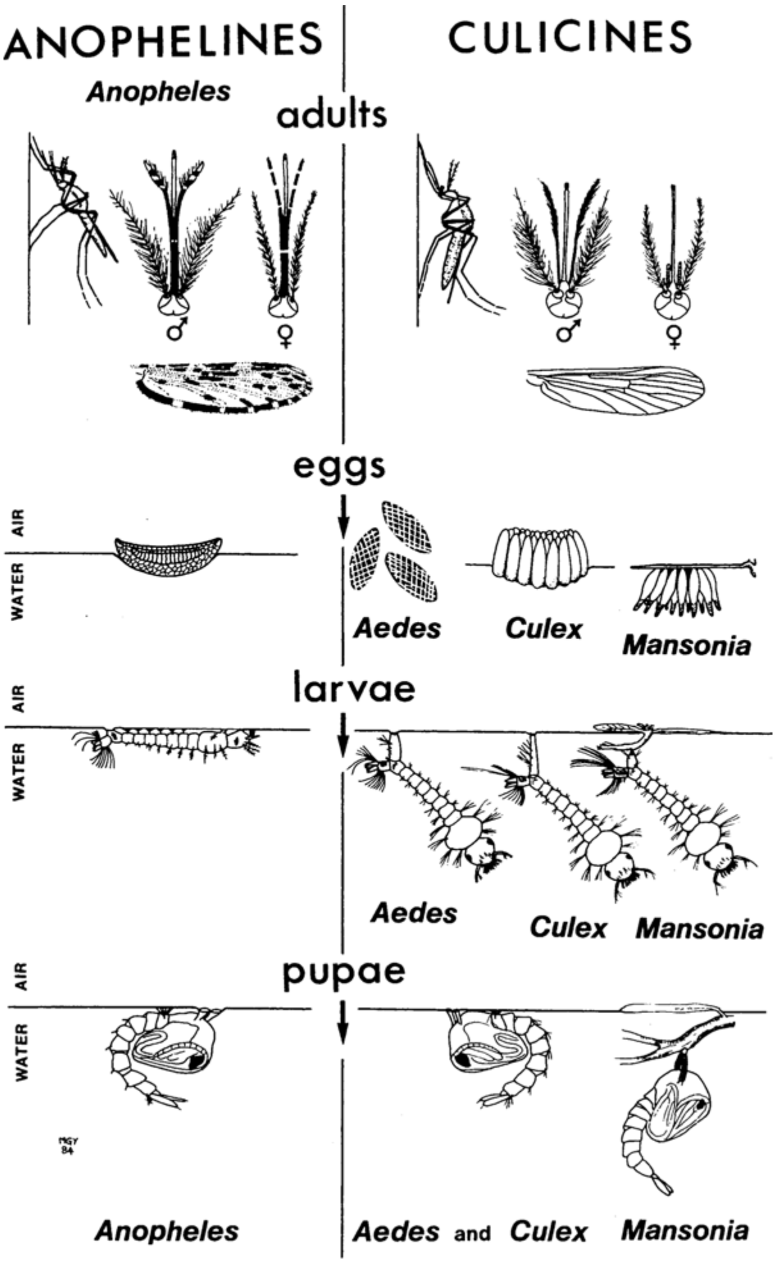


Figure 1.13 Chart of the principal characters of the stages in the life cycle that distinguish anopheline from culicine mosquitoes.

Table 1.1 *Principal characters distinguishing anopheline and culicine mosquitoes*

Stage	Anophelinae	Culicinae
Eggs	Laid singly, possess floats	Laid singly or in egg rafts or masses. Never possess floats
Larvae	Never have a siphon. Lie parallel to water surface. Have abdominal palmate hairs and tergal plates	All larvae have a short or long siphon. Subtend an angle from the water surface. No palmate hairs or tergal plates
Pupae	Breathing trumpets short and broad apically. Short peg-like spines on abdominal segments 2–7 or 3–7	Breathing trumpets short or long, opening not broad. No spines on abdominal segments 2–7
Adults (both sexes)	Rest at an angle to any surface. In most species dark and pale scales on wing veins arranged in distinct 'blocks'	Rest with body more or less parallel to the surface. Scales on wing veins not arranged in 'blocks'; scales frequently all brown or blackish, or a mixture of pale and dark scales scattered on veins
Adult females (non-plumose antennae)	Palps about as long as proboscis	Palps much shorter than proboscis
Adult males (plumose antennae)	Palps about as long as proboscis and swollen at ends	Palps about as long as proboscis but never swollen at ends; palps may be hairy distally

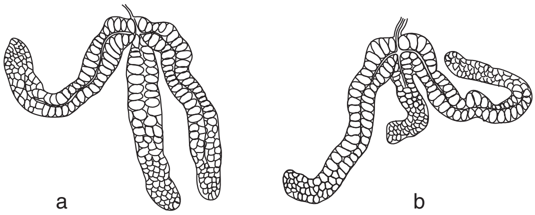


Figure 1.14 Salivary glands of adult mosquitoes: (a) culicine; (b) *Anopheles*. (Courtesy of Miss M. A. Johnson, and Blackwell Publishing, Oxford, publishers of *Entomology for Students of Medicine* (1962) by R. M. Gordon and M. M. J. Lavoipierre.)

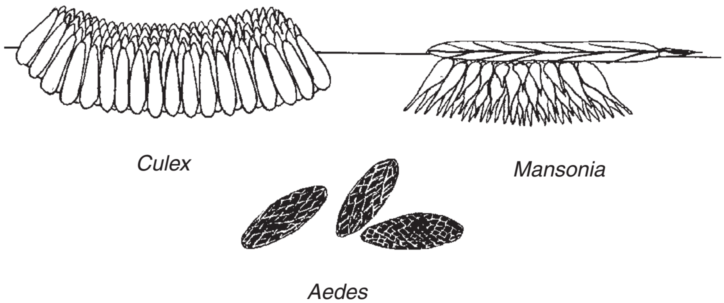


Figure 1.15 Mosquito eggs: *Culex* egg raft that floats on the water surface, *Mansonia* eggs glued to the undersurface of floating aquatic vegetation, and individual *Aedes* eggs that are deposited on damp surfaces.

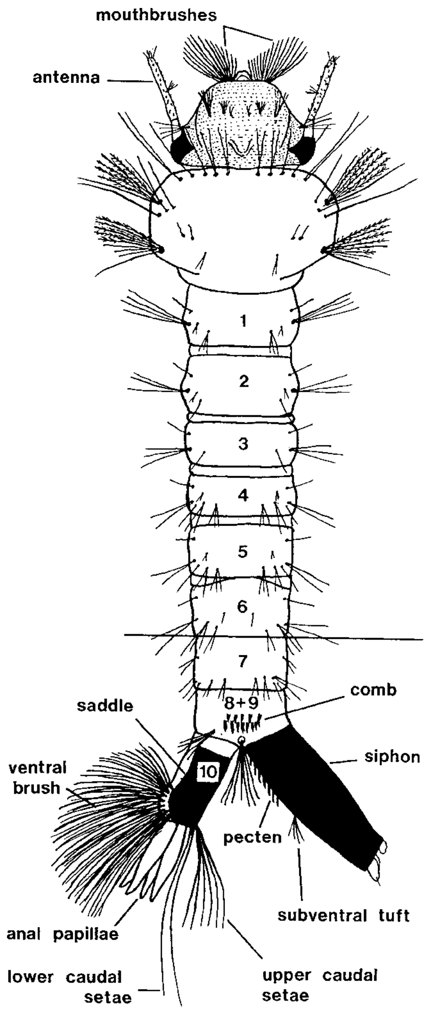


Figure 1.16 Culicine larva, dorsal view but with abdominal segments 7–9 turned laterally to display important identification features.

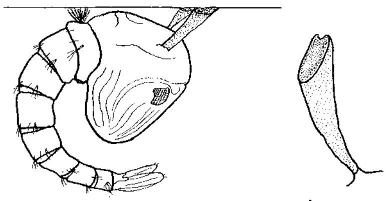


Figure 1.17 Culicine pupa: (a) pupal position at the water surface; (b) one of the two elongated and relatively narrow respiratory trumpets.

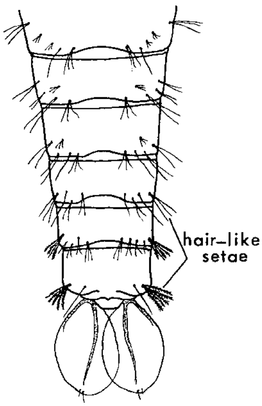


Figure 1.18 Part of the abdomen of a culicine pupa, showing hair-like setae. Note absence of lateral spines as found on anopheline pupae.

Culicine pupae

The length of the respiratory trumpets in culicine pupae is variable, but they are generally longer, more cylindrical and have narrower openings (Fig. 1.17) than in *Anopheles*. Abdominal segments 2–7 lack peg-like spines, although they have numerous setae (Fig. 1.18).

Culicine adults

Culicine adults rest with the thorax and abdomen more or less ***parallel*** to the surface (Fig. 1.13). The scales covering the wing veins are commonly uniformly brown or black. Sometimes there are contrasting dark and pale scales, but they are not arranged in distinctive areas or 'blocks', as found in many *Anopheles* adults.

The most reliable method for identifying the Culicinae is to examine their ***heads***. In females (which have non-plumose antennae) the ***palps*** are shorter than the proboscis. In males (which have plumose antennae) the ***palps*** are about as long as the proboscis but are not

swollen distally and hence do not appear clubbed (Fig. 1.13). However, the palps may be turned upwards distally, and in many species they are covered with long hairs so that superficially they can appear to be somewhat swollen apically, but more careful examination shows that the palps in male culicines are not clubbed as they are in *Anopheles*.

Other differences separating the Culicinae from *Anopheles* are that in culicines there are two or three spermathecae in females, but just one in anophelines. Also in culicines the middle lobe of the salivary glands is about as long as the other two, whereas in anophelines it is shorter (Fig. 1.14).

1.4 Medical importance

Although in several temperate countries mosquitoes may be of little or no importance in transmitting diseases to humans they can, nevertheless, cause considerable annoyance because of their troublesome bites. The greatest numbers of mosquitoes are found in the northern areas of the temperate regions, especially near or within the Arctic Circle, where the numbers biting can be so great at certain times of the year as to make almost any outdoor activity impossible. Because of their elongated mouthparts female mosquitoes can easily bite through clothing such as socks, shirts, blouses, trousers and woollen garments, but clothing with a much closer weave may prevent biting.

Mosquitoes are important as vectors of malaria, various forms of filariasis and numerous arboviruses such as dengue, yellow fever and West Nile virus. Their role in the transmission of these diseases is discussed in Chapters 2 and 3.

1.5 Mosquito control

Control measures which are directed against specific vectors, such as anopheline malaria vectors, and *Aedes aegypti* and *Culex quinquefasciatus*, are described in more detail in Chapters 2 and 3; only the more basic principles of control are outlined here.

Control measures can be directed at either the immature aquatic stages or the adults, or at both stages simultaneously.

1.5.1 Control directed at the immature stages

Biological control

Although often termed naturalistic control, there is little that is natural about biological control. Either the numbers of predators, parasites or pathogens in larval habitats must be greatly increased to obtain

worthwhile control, or they have to be introduced into habitats from which they were originally absent; such environmental manipulations are not natural. Biological control of mosquitoes was very popular during the early twentieth century, but with the availability of powerful insecticides it was largely replaced by chemical control. However, because of insecticide resistance and greater awareness of environmental issues there has been renewed interest in biological (biocontrol) methods. They are, however, usually more difficult to implement and maintain than insecticidal methods. Moreover, with predators it is unlikely that they will prey exclusively on mosquito larvae and pupae but will also eat harmless or even beneficial insects. Finally, biological control does not lead to rapid control. It takes some days, or more often weeks, before mosquito populations are substantially reduced in size.

Predators Larvivorous fish are the most widely used biological control agents, the most common being the top minnow or mosquitofish (*Gambusia affinis*). This is a warm-water fish originally native to the southern USA and northern Mexico but which has been introduced to some 60 countries, including the Pacific islands, Europe, the Middle East, India, Southeast Asia and Africa, in attempts to control mosquito larvae. They are aggressive fish which have sometimes destroyed indigenous species; consequently they should not now be introduced into new areas. Another commonly used fish is the South American guppy (*Poecilia reticulata*), which is not so voracious as *G. affinis* but can better tolerate low levels of organic pollution and is more heat-tolerant. There are numerous other fish that have been used to eat mosquito larvae, such as carp (e.g. *Cyprinus carpio* and *Ctenopharyngodon idella*) in Chinese ricefields, an edible catfish (*Clarias fuscus*) in water-storage tanks in Myanmar to control *Aedes aegypti*, *Oreochromis* (= *Tilapia*) species in Africa and *Aplocheilus* species in Asia.

Predatory fish, such as *Aphanius dispar* and *Fundulus* species, occur in saline waters and can therefore be introduced into saltwater habitats. Fish are unsuitable for controlling mosquitoes in small water containers and in pools and puddles that rapidly dry out. However, some fish, such as species of *Nothobranchius* and *Cynolebias*, which are the so-called instant or annual fish, have drought-resistant eggs, and these are more suitable for introducing into small temporary habitats that repeatedly dry out.

Although fish have sometimes greatly reduced the numbers of larvae in certain habitats, such as borrow pits, ponds, wells and ricefields, other than in parts of India and China they have rarely proved effective in reducing mosquito populations over relatively large areas. Nor is there usually much convincing evidence that they have significantly decreased the incidence of mosquito-borne diseases – but see Chapter 2 (page 48) in relation to malaria. However, in New Jersey, USA, a biocontrol company routinely

uses five species of reared larvivorus fish in its mosquito control programme.

Other predators of mosquito larvae include tadpoles of frogs and toads and various aquatic insect larvae, but these have rarely proved effective as control agents. There has been interest in predaceous copepods such as *Mesocyclop*s species to control larvae in water containers such as tyres, but the impact is usually very localized. Nevertheless, in New Jersey and New Orleans, USA, the predaceous copepod *Macrocyclops albidus* is being used to control mosquitoes. A few mosquitoes, such as *Toxorhynchites* species, have predaceous larvae that have sometimes been introduced to control mosquito larvae in container-habitats such as tree-holes, but results have not been very encouraging.

Pathogens and parasites There are numerous pathogens, such as iridescent and cytoplasmic polyhedrosis viruses, protozoans (e.g. *Bracheola* (= *Nosema*) *algerae* and *Vavraia culicis*) and fungi (e.g. species of *Coelomomyces*, *Lagenidium* and *Culicinomyces*) that cause larval mortality. There are also several parasitic nematodes that kill mosquito larvae; the best known is *Romanomermis culicivorax*, which was commercially mass-produced, but because of non-viable sales is no longer commercially available. None of these biological agents has given satisfactory control of mosquitoes.

In contrast, *Bacillus thuringiensis* var. *israelensis* (*Bti*) is undoubtedly the most effective pathogen, as it can be easily mass-produced, is toxicologically safe to humans and wildlife, and is more or less specific in killing mosquito larvae (but it also kills simuliids: see Chapter 4). It is commonly formulated as slow-release briquettes that float on the water surface and can give control for up to about 30 days. Sometimes *Bti* is formulated as a powder that is mixed with water and sprayed on larval habitats, but because there is no multiplication of the bacteria there must be repeated applications, as with most chemical larvicides. When *Bti* is ingested, mortality is caused by an endotoxin acting as a stomach poison.

Bacillus sphaericus can be formulated much as for *Bti* and kills mosquito larvae in a similar fashion, but differs in that in some situations it can recycle in larval habitats. This species is also more effective in organically polluted waters and is especially effective against *Culex* species. Both these *Bacillus* species are more like a microbial insecticide than a true biological (living) agent that recycles and maintains itself in the environment.

Resistance to both *Bti* and *B. sphaericus* has been observed in laboratory colonies of a few mosquito species, especially *Culex quinquefasciatus*. Although field populations of *Cx. pipiens* were recorded in New York State as being resistant to *Bti*, no resistance was recorded in field populations of *Aedes vexans* in Germany that had been exposed to *Bti* for over

25 years. Field populations of *B. sphaericus* have been reported as developing resistance in several countries including Brazil, China, India and Thailand, but *Bti* and *B. sphaericus* continue to be widely used. Recently genetic engineering techniques, such as the development of recombinant strains of these two bacteria, seem to have improved the larvicidal activity of the bacteria, and in addition the genes responsible for production of the poisonous endotoxin have been transferred to other bacteria.

Genetic control

Although genetic control methods are directed against the adults, it is convenient to discuss this strategy here because it is really a form of biological control.

There are basically two approaches to genetic control. One involves releasing into the field male mosquitoes that have been laboratory-reared and sterilized by a variety of techniques, such as with ionizing radiation, crossing closely related species to produce infertile hybrid males, or introducing chemosterilants into insectary rearing programmes which make emerging adults (both sexes) sterile. Large numbers of sterile males released into field populations will hopefully compete with natural fertile males for female mates, resulting in large numbers of infertile inseminations. Eggs layed by such females are sterile and fail to hatch. In El Salvador *Anopheles albimanus*, an important malaria vector, had developed resistance to most insecticides so in the 1970s about 4.36 million chemosterilized males were released into an isolated coastal region of about 15 km^2. More than a 97% reduction in the biting population was achieved. However, because enormous numbers of mosquitoes had to be reared to obtain control over a very small area there was later little interest in such methods. More recently this approach has been used against the vector of dengue (see Chapter 3, page 80).

The second approach aims at introducing into field populations species or strains of mosquitoes that are incapable of transmitting diseases. In 2010 a transgenic *Anopheles stephensi* was created that had both a reduced life span and complete resistance to infection with *Plasmodium falciparum*. However, mechanisms have to be found to drive the genes through wild populations when the transgenic mosquitoes are released into field populations of a vector.

Neither of these genetic approaches is simple, and they will be much more difficult to implement than conventional insecticidal methods. Nevertheless, there has been some progress in developing transgenic *Anopheles* species that are refractory to malaria parasites and *Aedes aegypti* mosquitoes that are unable to transmit dengue viruses.

Physical control

Filling in, source reduction and drainage This is sometimes referred to as mechanical or environmental control. A simple approach is to fill in larval habitats and thus completely eliminate them. Larval habitats ranging in size from water-filled tree-holes to ponds and small marshes can be filled in with rubble, earth or sand. However, filling in tree-holes can be problematic because many are at considerable heights and difficult to locate, or there can be too many for this method to be practical. Various container-habitats such as abandoned tin cans, metal drums, disused water-storage pots and old tyres can be removed: this approach is often referred to as ***source reduction***. Mosquito breeding in water-storage pots that are in use can be reduced by covering up their openings, but this simple practice is often not popular and it soon becomes neglected. Introduction of a reliable piped water supply should help reduce people's dependence on water-storage containers and thereby reduce breeding of mosquitoes such as *Aedes aegypti*. However, in many areas with piped water people continue to store water in containers as insurance against an unreliable water supply. In the Indian subcontinent water tanks are commonly sited on rooftops, and these are important breeding places of the vector (*Anopheles stephensi*) of urban malaria. Fitting these with mosquito screening would prevent breeding, but such covers usually become torn or are removed.

Some mosquitoes, such as *Culex quinquefasciatus*, breed in damaged septic tanks and soakaway pits, but this is easily prevented if the tanks and pits are repaired so that egg-laying females cannot gain access. This mosquito also commonly breeds in pit latrines, but this can be stopped if small (2–3 mm) expanded ***polystyrene beads*** are tipped into latrines to form a floating layer about 1–2 cm thick. This suffocates larvae and pupae and also prevents mosquitoes laying their eggs on the water surface. In Zanzibar and India such beads substantially reduced *Cx. quinquefasciatus* breeding in pit latrines and soakage pits and contributed greatly to the prevention of a resurgence of bancroftian filariasis following mass drug treatment.

Larval habitats such as ponds, borrow pits, freshwater and saltwater marshes can be drained. An advantage of filling in, draining or removing larval habitats is that this can lead to permanent control, but this approach is not always feasible. It is impossible, for example, to fill in all the scattered, small and temporary collections of water such as pools, vehicle tracks and puddles which often appear during the rainy season. Larger and more permanent habitats such as swamps may prove too costly to drain. Moreover, the local people may, understandably, not want certain breeding places filled in if the water is needed for domestic purposes or the sites used as watering points for livestock. The feasibility of eradicating breeding places must be assessed individually in each area.

Environmental manipulation If it is not feasible to eliminate mosquito larval habitats it may be possible to alter them to make them unsuitable for mosquitoes. For example, some mosquitoes occur in isolated pools and small marshy areas formed at the edges of ditches and streams having winding courses. Realigning these water courses to increase water flow and prevent the build-up of static pockets of water can greatly reduce mosquito breeding. The periodic opening of sluice gates can flush out larvae from small isolated pools of water. Other environmental modifications include the removal of overhanging vegetation to reduce breeding by shade-loving mosquitoes; conversely, planting vegetation along reservoirs and streams may eliminate sun-loving species. Intermittent flooding of ricefields to allow drying out every 3–5 days can substantially reduce populations of several important vectors. Removal of rooted or floating vegetation will prevent breeding of *Mansonia* species, because they require plants to obtain their oxygen requirements.

Instead of draining marshy areas, they can be excavated to form areas of relatively deep permanent water with well-defined vertical banks. This process is called ***impoundment***. It makes the habitat unsuitable for many mosquitoes, especially *Aedes* and *Psorophora* species, which lay their eggs on wet muddy edges of pools that are scattered over extensive marshy areas. Both small and large freshwater and saltwater marshy areas can be converted into impounded waters. Sometimes such impounded waters are stocked with fish and ducks, which will feed, to some extent, on mosquito larvae.

There is the danger, however, that larval habitats modified to reduce breeding of certain mosquito species may create conditions that support other mosquito species that were previously either absent or uncommon.

Chemical control

Most control directed against mosquitoes, except malaria vectors, consists of the application of larvicides.

Oils Spraying oils such as diesel and kerosene (paraffin) to kill mosquito larvae has been practised for over 100 years. The addition of detergents or vegetable oils increases the spreading power of oils, thus allowing application rates to be reduced. Although such oils may sometimes still be used, formulated commercial high-spreading oils which are environmentally more friendly are increasingly used. Dosage rates are commonly 9–27 litres per hectare or less. Other larvicides commonly used are monomolecular films of ethoxylated isostearyl alcohol derived from plant oils (commercial names are Arosurf, Agnique), which interfere with the properties of the air–water interface and cause larvae, pupae and even both emerging and ovipositing adults to drown.

Oils have to be sprayed on larval habitats about every 7–10 days in most tropical countries to ensure that larvae hatching from eggs are killed before they pupate and give rise to adults. Less frequent applications are made in cooler temperate areas because the aquatic life cycle is much longer.

Insecticides With the availability of insecticides such as DDT in the mid 1940s, oiling was largely replaced with spraying larval habitats with these more modern chemicals. However, because of their persistence in the environment and accumulation in food chains, DDT and other organochlorine insecticides should not now be used as larvicides. Less persistent and biodegradable insecticides should be used.

Recommended chemicals for larviciding include malathion, chlorpyrifos, fenthion and temephos. Pyrethroids such as permethrin and deltamethrin can also be used as larvicides, but because they tend to kill greater numbers of other aquatic insects, crustaceans and even fish they should be used with caution and only in special circumstances. In organically polluted waters insecticides are less effective, and so either higher dosage rates must be used or the more effective organophosphates such as fenthion or chlorpyrifos applied. Chlorpyrifos is more toxic to mosquito larvae than many other insecticides, but also causes higher mortalities of fish and other aquatic organisms, so needs to be used with caution.

All the above insecticides usually have to be ***sprayed*** on larval habitats in tropical areas every 10–14 days, and more frequently on highly polluted waters.

Because temephos has a very low mammalian toxicity, 1% sand granules or microencapsulated formulations, which slowly release the insecticide over days or even weeks, can be placed in containers holding potable water to control *Aedes aegypti*. This gives a concentration of 1 mg active ingredient per litre of water. However, people have sometimes refused to have their water pots treated with temephos, either because of the unpleasant odour or (understandably) because they consider any insecticide in drinking water as environmental contamination. This attitude is likely to spread. In addition, there are suggestions that temephos could be toxigenic and mutagenic.

Mansonia larvae can be killed by spraying herbicides to destroy the aquatic vegetation on which they rely to obtain their oxygen.

Larvicides are usually applied as emulsions or oil solutions, but granules, pellets or gelatine capsules, often containing pyrethroids, can be used to penetrate dense growths of aquatic vegetation. Insecticides formulated as ***slow-release*** granules or pellets can be scattered over marshy areas when they are relatively dry, then when they become flooded larvae hatching from drought-resistant aedine eggs, such as those of *Aedes* and *Psorophora* species, are killed as the granules release their toxicants into the water. Larvicides are usually delivered from knapsack-type sprayers carried on the backs of operators, but they are sometimes dispersed from

vehicle-mounted spraying machines. Large or inaccessible areas may require aerial spraying from helicopters or small fixed-wing aircraft.

Insect growth regulators (IGRs)

These are compounds, such as methoprene, fenoxycarb and pyriproxyfen, that arrest larval development of insects, or compounds such as diflubenzuron and novaluron, which inhibit chitin formation in the immature stages. When used as larvicides these chemicals have the benefit of being environmentally friendly, because they are more or less specific in killing mosquitoes and possess extremely low toxicity to humans. Many IGRs can be formulated as liquids, granules or briquettes which can give control for more than 100 days. However, their relatively high cost may limit their use in poorer countries.

Although mosquitoes have not been reported as developing resistance to IGRs, low-level resistance has been found in *Musca domestica* and *Lucilia cuprina*, the sheep blowfly.

Integrated control

It has become fashionable to advocate ***integrated*** control, which usually means combining biological and insecticidal methods: for example, the introduction of predaceous fish to breeding places which are also sprayed with insecticides that have minimum effect on the fish. However, it is better to regard integrated control as any approach that takes into consideration more than one method, whether these are directed at only the larvae or the adults, or both.

1.5.2 Control directed at adults

Personal protection

Much can be done to reduce biting by mosquitoes. Houses, hospitals and other buildings can have windows and doors covered with mosquito screening, made of either strong plastic or non-corrosive metal. It is essential that screening is kept in good repair. Screens of 6–8 mesh (i.e. 6–8 holes/cm) will exclude most mosquitoes. Finer-mesh screening will keep out smaller biting flies, some of which may be vectors, but will appreciably reduce ventilation and light. If houses are unscreened, or if screening is defective, ***mosquito nets*** can be used to protect against night-biting mosquitoes. Nets should be tucked in under mattresses or bedding, never allowed to drape loosely over beds. Torn nets are useless unless they have been impregnated with pyrethroid insecticides (see Chapter 2, page 50). Nets should be placed over beds before sunset. The main disadvantage of nets is that they can reduce ventilation.

Small spray-guns (e.g. flit-guns) filled with solutions of pyrethrum or permethrin can be used to spray bedrooms early in the evenings to kill

resting mosquitoes, but pressurized aerosol canisters containing pyrethroids have replaced flit-guns in many parts of the world, although they are more expensive. Mosquito coils impregnated with pyrethroid insecticides, especially fast-acting ones such as bioallethrin, which when ignited smoulder for 6–10 hours to produce an insecticidal smoke, are commonly used in tropical countries. A more sophisticated, but more expensive, method is to place small insecticide-impregnated tablets (called vaporizing or fumigant mats) on a mains-operated electric mini-heater, giving protection for up to 8–12 hours.

An effective repellent is DEET, which has been used for over 50 years. Although it has periodically been suggested that it may cause side effects, most people apply it infrequently and are consequently exposed to very low dosages. In brief, people can still use DEET, although more recently repellents based on piperidines have become available, marketed under the names of Autan, Cutter Advanced, Bayrepel, Picaridin and Icaridin. These piperidine-based repellents are about as effective as DEET, but unlike DEET they do not attack plastics. Under optimal conditions these repellents can provide protection for 6–10 hours, the duration depending on the quantity of active ingredient.

Citronella oil and lemon eucalyptus oil can give protection against mosquitoes, but only for about an hour. A new botanical repellent known as PMD (para-menthane-3,8-diol), derived from lemon eucalyptus, is recognized as the only botanical repellent that gives good protection from mosquito bites.

Repellents are applied to the hands, arms, neck and face (taking care to avoid the eyes), and the ankles and legs, irrespective of whether socks or long trousers are worn. Sweating and rubbing usually reduce the period of effectiveness of repellents. Repellent- or insecticide-impregnated (e.g. permethrin or allethrin) clothing, such as wide-mesh jackets and hoods (as used by military personnel) give longer protection than repellents applied to the skin. If treated clothing is kept in plastic bags when not in use it should remain effective for many months before re-impregnation is needed.

Aerosols, mists and fogs

Motorized knapsack mist-blowers, shoulder-carried thermal foggers or boat- or vehicle-mounted machines that generate insecticidal aerosols (< 50 µm) or mists (51–100 µm) can be used to kill outdoor-resting (exophilic) adult mosquitoes. Fogs are produced when very fine aerosol droplets (5–15 µm) are so numerous that they substantially reduce visibility. Indoor-resting (endophilic) adults are also occasionally killed by mist-blowers or thermal foggers. Several insecticides can be used, including organophosphates and pyrethroids. Although such applications can be

spectacular, and please the public, there is very little residual effect. Areas cleared of adult mosquitoes are rapidly invaded by newly emerged adults and mosquitoes flying in from outside the treated area. Repeated applications are needed to sustain control.

Applications of aerosols and mists are best made in calm weather, and usually in the evenings or early mornings when there are fewer thermals rising from the ground and less turbulence. Aerial applications from helicopters or fixed-wing aircraft usually give better coverage and more effective control than ground-based operations.

Ultra-low-volume applications Ultra-low-volume (ULV) techniques apply the minimum of concentrated insecticides, often just 150–400 ml/ha, as against 5–25 litres/ha with conventional spraying. This allows trucks or aircraft to spray much larger areas with a tank of insecticide before the tank needs refilling. Insecticides commonly used include organophosphates and pyrethroids. With aerial applications ***droplet size*** of the insecticide is bigger (150–200 µm) than that used in ground-based applications (50–100 µm) because they decrease in size, due to evaporation, as they fall to the ground. Generally the size of droplets hitting mosquitoes should be 15–25 µm. In addition to rapidly reducing outdoor resting and biting mosquitoes, ULV spraying is used in potential or actual epidemic situations to prevent or control disease outbreaks. In emergency situations aerial spraying gives fast and effective vector control, and has been used to stop transmission of dengue, Japanese encephalitis, and in North America various encephalitis viruses.

Indoor residual spraying (IRS)

Some mosquitoes, such as many malaria vectors and *Culex quinquefasciatus*, rest in houses before and/or after blood-feeding. Their populations can be reduced by insecticidal spraying of houses, but as this approach is mainly used in malaria control operations it is described in Chapter 2.

It should be emphasized that most countries have legislation regulating what insecticides can be used against pests and vectors, and this may not necessarily be in accordance with WHO proposals.

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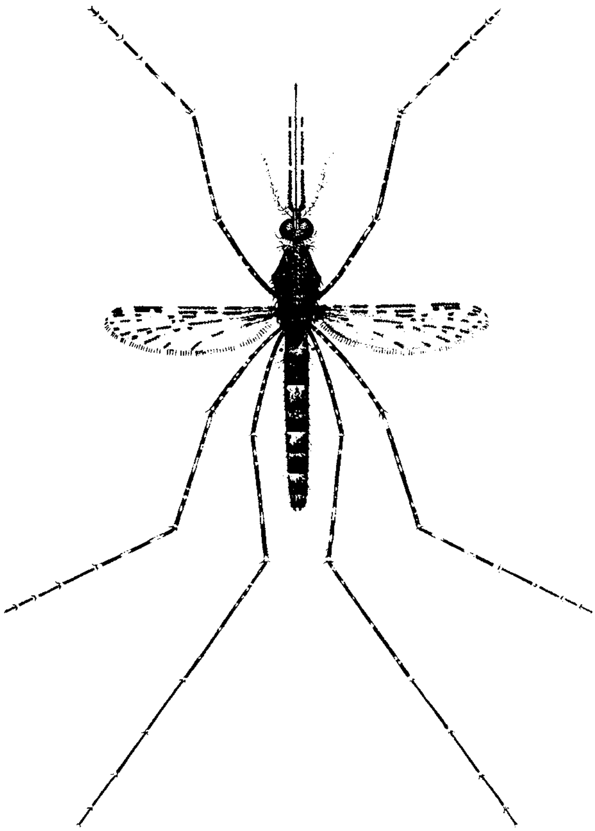
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See also references at the ends of Chapters 2 and 3.

2

Anopheline mosquitoes (Anophelinae)



The subfamily Anophelinae contains three genera, but as explained in Chapter 1 only the genus *Anopheles* is of medical importance. *Anopheles* mosquitoes have an almost worldwide distribution, occurring in both tropical and temperate regions, but they are absent from most Pacific islands including New Zealand. There are about 476 species. The most important disease transmitted by *Anopheles* mosquitoes is malaria. Some *Anopheles* species are vectors of filariasis, especially that caused by *Wuchereria bancrofti*, but other species transmit *Brugia malayi* and *Brugia timori*. A few species transmit arboviruses that are mainly of minor medical importance.

2.1 External morphology

The main features distinguishing the Anophelinae from the Culicinae have been given in Chapter 1, but are briefly summarized here.

Anopheline eggs are laid singly and have air-filled ***floats*** (Fig. 1.8) that help them float on the water surface.

Larvae do not have a siphon and consequently lie ***parallel*** to the water surface (Fig. 1.13). A ***tergal plate*** and paired ***palmate hairs*** are present dorsally on most abdominal segments (Fig. 1.9).

Pupal abdominal segments have numerous short setae, and segments 2–7 or 3–7 have in addition short peg-like spines (Fig. 1.11) which are absent in culicines.

Most, but not all, adult *Anopheles* have ***spotted wings***, that is the dark and pale scales are arranged in small blocks or areas on the veins (Fig. 1.12, Plate 1). The number, length and arrangement of these dark and pale areas differ considerably in different species and provide useful characters for species identification. Unlike culicines, the dorsal and ventral surfaces of the abdomen are almost, or entirely, devoid of appressed scales. In both sexes the ***palps*** are about as long as the proboscis, and in males, but not females, they are enlarged (i.e. clubbed) apically (Fig. 1.13). See Chapter 1 (page 14) for minor differences distinguishing anophelines from culicines.

2.2 Life cycle

After mating and blood-feeding *Anopheles* lay some 50–200 small brown or blackish boat-shaped eggs (Fig. 1.8) on the water surface. *Anopheles* eggs cannot withstand desiccation and in tropical countries hatch within 2–3 days, but in colder temperate climates hatching may not occur until after about 2–3 weeks, the duration depending on temperature.

As in all mosquitoes there are four larval instars. *Anopheles* larvae are filter-feeders and unless disturbed remain at the water surface, feeding on bacteria, yeasts, protozoans and other microorganisms. When feeding, larvae rotate their heads through 180 degrees so that the ventrally positioned mouthbrushes can sweep the underside of the water surface. Larvae

are easily disturbed by shadows or vibrations and respond by swimming quickly to the bottom of the water. They resurface some seconds or minutes later. Unlike culicine larvae, they lack a siphon and so breathe in air through their posterior spiracles.

Anopheles larvae occur in many different types of more or less permanent habitats, ranging from freshwater and saltwater marshes, mangrove swamps and ricefields to grassy ditches, wells, edges of streams and rivers as well as ponds and borrow pits. Larvae are also found in small and often temporary habitats such as puddles, hoofprints, discarded tin cans and sometimes water-storage pots. A few species occur in water-filled tree-holes. In the Neotropical region (Central and South America and the West Indies) a few *Anopheles* breed in water that collects in the leaf axils of epiphytic plants such as ***bromeliads***, which somewhat resemble pineapple plants, but grow on tree branches. Some *Anopheles* prefer habitats with aquatic vegetation while others favour waters without vegetation; some species like exposed sunlit waters whereas others prefer more shaded larval habitats. In general *Anopheles* are found in clean and unpolluted waters, usually being absent from habitats containing rotting plants or faeces.

In tropical countries the larval period frequently lasts only about 7 days, but in cooler climates the larval period may be 2–4 weeks. In temperate areas some *Anopheles* overwinter as larvae and consequently may live many months.

The comma-shaped pupae normally remain floating at the water surface, but when disturbed they swim vigorously down to the bottom with characteristic jerky movements. The pupal period lasts 2–3 days in tropical countries but sometimes as long as 1–2 weeks in cooler climates, after which the adult mosquito emerges.

2.2.1 Adult biology and behaviour

Most *Anopheles* are ***crepuscular*** or ***nocturnal*** in their activities. Thus blood-feeding and oviposition normally occur in the evenings, at night or in the early mornings around sunrise. Some species, such as *An. albimanus*, a malaria vector in Central and South America, bite people mainly outdoors (***exophagic***) from about sunset to 21:00 hours. In contrast, in Africa species of the *An. gambiae* species complex, which contains probably the world's most efficient malaria vectors, bite mainly after 23:00 hours to just before sunrise, and this is mostly indoors (***endophagic***). As already discussed in Chapter 1, the times of biting, and whether adult mosquitoes are exophagic or endophagic, may be epidemiologically important.

Both before and after blood-feeding some species rest in houses (***endophilic***), whereas others rest outdoors (***exophilic***) in a variety of shelters, such as amongst vegetation, in rodent burrows, in cracks and crevices in trees, under bridges, in termite mounds, in caves and rock fissures, and in cracks in the ground. Most *Anopheles* species are not exclusively exophagic or

endophagic, exophilic or endophilic, but exhibit a mixture of these extremes of behaviour. Similarly, few *Anopheles* feed exclusively on either humans or non-humans, most feeding on both people and animals, but the degree of anthropophagism and zoophagism varies according to species. For example, *An. culicifacies*, an important Indian malaria vector, commonly feeds on cattle as well as humans, whereas in Africa *An. gambiae* s. str. (a species of the *An. gambiae* species complex) feeds more infrequently on cattle and thus maintains a stronger mosquito–human contact. This is one of the reasons why *An. gambiae* is a more efficient malaria vector than *An. culicifacies*.

2.3 Medical importance

2.3.1 Biting nuisance

Although *Anopheles* mosquitoes may not be disease vectors in an area they may nevertheless be a biting nuisance. Usually, however, it is culicine mosquitoes, especially *Aedes* and *Psorophora* species, that cause biting problems.

2.3.2 Malaria

Only mosquitoes of the genus *Anopheles* transmit the parasites causing human malaria. The most important malarial parasites are *Plasmodium falciparum*, *P. vivax*, *P. malariae* and *P. ovale*, but recently it was discovered that a fifth species, *P. knowlesi*, which infects mainly macaque monkeys (*Macaca* species) in South Asia, can also cause malaria in humans. Because the sexual cycle of the malaria parasite occurs in the vector, it is conventional to call the mosquito the ***definitive host***, and humans the intermediate host.

Male and female malaria gametocytes ingested by female mosquitoes during blood-feeding pass to the mosquito's stomach, where they undergo cyclical development that includes a sexual cycle termed sporogony. Only ***gametocytes*** survive in the mosquito's stomach; all other blood forms of the malaria parasites (the asexual forms) are destroyed. Male gametocytes (microgametocytes) extrude flagella which are the male gametes (microgametes), and the process is called ***exflagellation***. The microgametes break free and fertilize the female gametes (macrogametes) which have formed from the macrogametocytes. As a result of fertilization a ***zygote*** is formed, which elongates to become an ookinete. This penetrates the wall of the mosquito's stomach and reaches its outer membrane, where it becomes spherical and develops into an ***oocyst***, which can be seen on the stomach walls of vectors about 4–5 days after an infective blood-meal. The nucleus of the oocyst divides repeatedly to produce numerous spindle-shaped ***sporozoites***. After about 8 days the oocyst is fully grown (about 40–80 μm) and ruptures to release thousands of sporozoites into the haemocoel of the mosquito. The sporozoites (10–15 μm) are carried in the

insect's haemolymph to all parts of the body, but most penetrate the ***salivary glands***, where they are usually found after 9–14 days. However, the time required for this cyclical development (***extrinsic cycle***) depends on both temperature and *Plasmodium* species. At 30 °C sporogony in *P. falciparum* takes 9 days, at 25 °C 10 days, and at 20 °C 23 days, while below 17 °C it cannot be completed. With *Plasmodium vivax* sporogony develops faster: it is completed in 9 days at 25 °C and in 16 days at 20 °C.

The mosquito is now ***infective***, and sporozoites are inoculated into people the next time the mosquito bites. A single oocyst produces 1000 or more sporozoites, and it has been estimated that in heavy infections there may be as many as 60 000–70 000 sporozoites in the vector's salivary glands. However, the number may be much smaller than this, and very few (sometimes just 5–10) are actually injected into a person during feeding.

The ***sporozoite rate***, that is the percentage of female vectors with sporozoites in their salivary glands, varies considerably from species to species of mosquito but also according to locality and season. Sporozoite rates are often about 1–5% in species such as *An. gambiae* and *An. arabiensis* of the *An. gambiae* species complex, but less than 1% in many other species such as *An. albimanus* and *An. culicifacies*. For practical purposes it can be said that once a vector becomes infective it remains so throughout its life.

2.3.3 Important malaria vectors

Although there are some 476 species of *Anopheles* only about 70 transmit human malaria, and of these probably only about 40 are important ones. Malaria vectors are often divided into primary and secondary vectors, but this can be misleading because a species may be considered a primary vector in some areas but only a secondary vector in others. Although presenting a list of important malaria vectors is somewhat subjective I have nevertheless attempted to do this, and I provide notes on their principal larval habitats and biting behaviour. These notes are only a guide to their behaviour, which may vary in different parts of a species' geographical range. Several species occur as species complexes, which comprise virtually identical-looking species that can be separated only by their chromosomal banding patterns, by biochemical procedures or by molecular methods. However, species within a complex may differ in their behaviour, distribution and vector status. The best known complex is probably the *An. gambiae* species complex. To give an example of the differences in biology and vector status that can occur in a species complex, mosquitoes of the *An. gambiae* complex are described next.

(1) Sub-Saharan Africa

Anopheles gambiae The most anthropophagic species and the most important malaria vector of the eight species comprising the *An. gambiae*

species complex is *An. gambiae* s. str. Larval habitats are sunlit pools, puddles, hoofprints, borrow pits and ricefields. Adults bite humans both indoors and outdoors, and also feed on domesticated animals. They rest mainly indoors, but sometimes outdoors. Other malaria vectors in the *An. gambiae* species complex are *An. arabiensis*, *An. melas*, *An. merus*, *An. bwambae*, *An. quadriannulatus* species A, *An. quadriannulatus* species B and *An. comorensis*, and these are very briefly discussed below.

Anopheles arabiensis Another important malaria vector. Larvae in the same habitats as *An. gambiae*. Adults bite humans indoors and outdoors but also cattle; after feeding they rest either indoors or outdoors. This species tends to occur in drier areas than *An. gambiae*, and is more likely to bite cattle and rest outdoors than *An. gambiae*.

Anopheles melas and An. merus *An. melas* is found in West Africa, where it occurs in coastal salt waters such as mangrove swamps, while *An. merus* is a coastal saltwater species in East and southern Africa, but can also be found breeding in inland saltwater habitats. Adults of both species bite humans and rest both indoors and outdoors; they are both regarded as secondary malaria vectors.

Anopheles bwambae A rare species restricted to breeding in the warm mineral springs in Semuliki National Park, Uganda. Not considered an important vector, although locally it can transmit malaria.

Anopheles quadriannulatus and An. comorensis *An. quadriannulatus* species A and B both feed on cattle and are not considered malaria vectors. The final member of the *An. gambiae* species complex is *An. comorensis*, a very rare species found only on Mayotte, Comoros archipelago; it is not considered to be a vector.

Anopheles funestus Larvae occur in more or less permanent waters, especially those with vegetation, such as marshes, edges of streams, rivers and ditches, and ricefields with mature plants providing shade. Prefers shaded habitats. Adults bite humans predominantly, but also domesticated animals. Feeds indoors and also outdoors; after feeding adults rest mainly indoors.

(2) Europe, North Africa and the Middle East

Anopheles atroparvus One of the species in the *An. maculipennis* species complex. Sunlit and exposed pools and ditches with either fresh or brackish water, also ricefields. Adults bite humans and domesticated animals and usually rest in stables, cowsheds and piggeries. Adults hibernate in these

and other shelters during the winter, but periodically emerge to take bloodmeals.

Anopheles labranchiae Another species in the *An. maculipennis* species complex. Brackish waters of coastal marshes, freshwater marshes, ricefields, edges of grassy streams and ditches; prefers sunlight. Bites humans and domesticated animals indoors and outdoors; rests mainly in houses or animal shelters after feeding. Overwinters as hibernating adults.

Anopheles pharoensis Marshes, ponds, especially those with abundant grassy or floating vegetation, also ricefields. Adults bite humans and animals indoors or outdoors, and rest outdoors after feeding.

Anopheles sacharovi Fresh or brackish waters of coastal or inland marshes, pools and ponds, especially those with vegetation. Prefers sunlit habitats. Bites humans and animals indoors or outdoors; usually rests in houses or animal shelters after feeding.

Anopheles sergentii Borrow pits, ricefields, ditches, seepage waters, slow-flowing streams, sunlit or partially shaded habitats. Adults bite humans or animals indoors or outdoors, resting in houses and caves after feeding.

Anopheles stephensi Probably a species within a complex. Can be an important vector locally, especially in towns. Apart from being found in Egypt, Iraq, Iran and Saudi Arabia it is common in the Indian subcontinent, where it is commonly the main vector of urban malaria. Larvae breed in fresh, brackish or even polluted waters in man-made habitats such as water tanks, cisterns, wells, gutters, water-storage jars and containers. Adults bite humans indoors or outdoors, and rest mainly indoors afterwards. *Anopheles stephensi* has a very wide distribution extending from the Middle East across Pakistan and India, to Myanmar, Thailand and China.

Anopheles superpictus Flowing waters such as torrents of shallow water over rocky streams, pools in rivers, muddy hill streams. Vegetation may be present; prefers sunlight. Bites humans and animals indoors and outdoors, and after feeding rests mainly in houses and animal shelters, but also in caves.

(3) Indian subcontinent

Anopheles annularis A species in the *An. annularis* species complex. Can be an important vector in India. Larvae in ponds, especially those with vegetation, swamps and ricefields. Adults bite humans and cattle outdoors and indoors, and rest mainly outdoors after feeding.

Anopheles baimai Pools, small streams, ditches, animal footprints, in partial sunlight or in forests. Bites humans both indoors and outdoors, and also domesticated animals; often enters houses to feed, but rests outdoors.

Anopheles culicifacies A species in the *An. culicifacies* species complex. Most important vector in the Indian subcontinent. Larvae in a variety of clean and unpolluted habitats, irrigation ditches, ricefields, pools, wells, borrow pits, edges of streams, marshes, and occasionally in brackish waters. Adults prefer domesticated animals but commonly bite humans indoors or outdoors; rests mainly indoors after feeding. The main malaria vector in much of the region.

Anopheles fluviatilis A species in the *An. fluviatilis* species complex. Flowing waters such as hill streams, pools in riverbeds, irrigation ditches, seepages; prefers sunlight. Bites humans and domesticated animals; feeds and rests either indoors or outdoors.

Anopheles minimus A species in the *An. minimus* species complex. Flowing waters such as foothill streams, springs, irrigation ditches, ricefields, seepages, borrow pits; prefers shaded areas. Feeds mainly on humans, but will bite domesticated animals; feeds and rests mainly indoors.

Anopheles stephensi See entry under Europe, North Africa and the Middle East.

Anopheles sundaicus A species in the *An. sundaicus* species complex. Salt or brackish waters including lagoons, marshes, pools and seepages, especially with putrefying algae and aquatic weeds. Mainly a coastal species, but found in freshwater inland pools in Java and Sumatra. Prefers sunlit habitats. Bites humans and domesticated animals indoors and outdoors; rests mainly indoors after feeding.

Anopheles superpictus See entry under Europe, North Africa and the Middle East.

(4) Southeast Asia

Anopheles aconitus A species in the *An. aconitus* species complex. Ricefields, swamps, irrigation ditches, pools and streams with vegetation; prefers sunlit habitats. Adults feed indoors or outdoors on humans but also commonly on cattle; rests indoors or outdoors after feeding.

Anopheles anthropophagus Shaded pools and ponds, only rarely in ricefields. Adults bite humans indoors and rest mainly indoors after feeding.

Anopheles baimai See entry under Indian subcontinent.

Anopheles balabacensis Muddy and shaded forest pools, animal hoof-prints and vehicle ruts, occasionally in deep wells. Adults bite humans and cattle and feed and rest outdoors. Morphologically and biologically very similar to *An. dirus*, but has a more restricted distribution – Sabah, Java, Borneo and certain Philippine islands.

Anopheles campestris A species in the *An. campestris* species complex. Deep and usually shaded or partially shaded waters such as ditches, wells, and shaded parts of ricefields, but also sometimes in brackish waters. Bites humans and animals indoors and outdoors, and rests indoors or outdoors after feeding.

Anopheles culicifacies See entry under Indian subcontinent.

Anopheles dirus A species in the *An. dirus* species complex. Shaded pools, hoofprints in or at the edges of forests. Adults bite humans and domesticated animals, mainly outdoors, and stay outdoors after feeding. Morphologically and biologically very similar to *An. balabacensis*, but has a more widespread distribution from western India and Bangladesh to Southeast Asia.

Anopheles donaldi Shaded habitats such as tree-covered swamps, forest pools, often with vegetation, ricefields. Bites domesticated animals but also feeds on humans inside or outside houses; rests mainly outdoors.

Anopheles flavirostris Flowing waters such as foothill streams, springs, irrigation ditches, also borrow pits and ricefields. Prefers shaded areas of sunlit habitats. Feeds mainly on humans, but also on domesticated animals; feeds indoors or outdoors but rests mainly outdoors after feeding.

Anopheles fluviatilis See entry under Indian subcontinent.

Anopheles latens Seepage pools, ground pools along stream margins, sandy pools in stream banks, shallow flowing streams and elephant foot-prints. Basically a forest species, biting people in forests or near forests in rubber plantations and orchards.

Anopheles letifer Often in acidic and stagnant pools, swamps and ponds, especially on coastal plains; prefers shade. Adults bite domesticated animals and humans mainly outdoors, and rest afterwards outdoors.

Anopheles leucosphyrus A species in the *An. leucosphyrus* species complex. Clear seepage pools in forests. Adults bite humans inside and outside houses, but afterwards rest outdoors. This species is morphologically and biologically similar to *An. balabacensis* and *An. dirus*.

Anopheles maculatus A species in the *An. maculatus* species complex. Seepage waters, pools formed in streams, rock-pools, edges of ponds, ditches and swamps with much vegetation; prefers sunlight. Bites humans and animals mainly outdoors and rests outdoors after feeding.

Anopheles minimus See entry under Indian subcontinent.

Anopheles nigerrimus Larvae in deep ponds, ricefields, irrigation ditches and marshes having much vegetation; prefers sunlight. Adults bite humans and animals mainly outdoors, and rest mainly outdoors.

Anopheles sinensis Has been often confused with *An. anthropophagus*. Common in China, where in some localities it may be a more important vector than *An. anthropophagus*. Also an important vector in Taiwan and Korea, but not in Indonesia, Malaysia and Thailand. Larvae in ricefields, marshes, ditches and grassy ponds. Adults bite cattle and humans, indoors or outdoors; rests indoors or outdoors.

Anopheles subpictus A species in the *An. subpictus* species complex. Muddy pools near houses, borrow pits, gutters, also brackish waters. Bites mainly animals, but also humans both indoors and outdoors; rests indoors or outdoors after feeding.

Anopheles sundaicus See entry under Indian subcontinent.

(5) Mexico and Central America

Anopheles albimanus Fresh or brackish waters such as pools, puddles, marshes, ponds, ricefields and lagoons, especially those containing floating or grassy vegetation; prefers sunlit habitats. Adults feed on humans and domesticated animals both indoors and outdoors; after feeding adults rest mainly indoors.

Anopheles albitarsis A species in the *An. albitarsis* species complex. Larvae usually in sunlit ponds, large pools and marshes with filamentous algae. Bites humans and domesticated animals almost indiscriminately. Feeds outdoors and also indoors, and usually rests outdoors after feeding.

Anopheles aquasalis Tidal saltwater marshes, lagoons, saltwater regions of rivers, estuaries, rarely in fresh water; sunlit or shaded habitats. Adults bite humans and domesticated animals indoors or outdoors; rests mainly outdoors.

Anopheles darlingi Freshwater marshes, lagoons, ricefields, swamps, lakes, ponds, pools, edges of streams, especially with vegetation. Mainly shaded larval habitats. Feeds mainly on humans indoors; stays indoors after feeding.

Anopheles pseudopunctipennis A species in the *An. pseudopunctipennis* species complex. Pools, puddles, seepage waters and edges of streams, especially habitats with algae; prefers sunlight. Feeds almost indiscriminately indoors or outdoors on humans and domesticated animals; rests outdoors.

Anopheles punctimacula Small pools, swamps, grassy pools at edges of streams; prefers shade. Bites humans and domesticated animals both indoors and outdoors; rests indoors or outdoors after feeding.

(6) South America

Anopheles albitarsis See entry under Mexico and Central America.

Anopheles aquasalis See entry under Mexico and Central America.

Anopheles bellator Larvae found only in water collected in the leaf axils of bromeliads, which are epiphytes on trees in the Americas. Adults bite humans during the day in shaded forests, and also at night, and may enter houses to feed. Adults rest mainly outdoors. The species will also bite domesticated animals. It occurs in Trinidad, Venezuela, Surinam, Guyana and Brazil, where it can be a local malaria vector.

Anopheles cruzii Another malaria vector that breeds in bromeliad axils. Adults bite humans indoors and outdoors, and rest indoors and outdoors. Mainly a malaria vector in coastal areas of Brazil.

Anopheles darlingi See entry under Mexico and Central America.

Anopheles nuneztovari A species in the *An. nuneztovari* species complex. Muddy waters of pools, vehicle tracks, hoofprints and small ponds, especially in and around towns; prefers sunlight. Feeds mainly on animals,

but in northern Colombia and western Venezuela adults bite humans indoors and outdoors, and rest outdoors after feeding.

Anopheles punctimacula See entry under Mexico and Central America.

(7) Australasia

Anopheles farauti A species in the *Anopheles farauti* species complex. Larvae usually in semi-permanent waters such as swamps, ponds, lagoons and edges of slow-flowing streams, but also in puddles, hoofprints, pools and rarely in man-made containers; water may be fresh or brackish and in sunlight or shade. Adults bite animals but also humans indoors or outdoors, and rest mainly outdoors, but also indoors.

Anopheles koliensis Larvae occur in marshy pools, irrigation ditches, pools at edges of forest streams, often in sunlit habitats. Adults bite humans and more occasionally animals, and after feeding rest mainly indoors, but they rest outdoors in some areas.

Anopheles punctulatus A species in the *An. punctulatus* species complex. Larvae occur in temporary and often muddy pools, puddles, hoofprints and ditches, usually in sunlight. Adults bite humans in preference to animals, and rest indoors or outdoors after feeding.

2.3.4 Filariasis

Certain *Anopheles* species transmit filarial worms of *Wuchereria bancrofti*, *Brugia malayi* and *Brugia timori*, all of which cause filariasis in humans. The role of culicine mosquitoes as vectors of the first two species is described in Chapter 3, and details of principal mosquito vectors are given in Table 3.1 (page 77).

Wuchereria bancrofti is the most widespread filarial infection of humans in many subtropical and tropical countries in Africa, Asia, the South Pacific and the Americas. In many of these areas bancroftian filariasis is mainly an urban disease. In contrast, *Brugia malayi* is more a rural disease and is restricted to South and Southeast Asia, occurring in countries such as southern India, Malaysia, Vietnam, Indonesia, Thailand, Papua New Guinea and the Philippines. It is absent from Africa and the Americas.

Both bancroftian and brugian filariasis occur in two basic forms: ***nocturnally periodic*** and ***nocturnally subperiodic***. Anophelines, together with certain culicines (*Culex quinquefasciatus*, various species of *Mansonia* and a very few *Aedes* species) are the vectors of the nocturnally periodic form. Culicines are vectors of subperiodic forms (see Chapter 3).

In the nocturnally periodic form of these two parasites most of the microfilariae during the day are in the blood vessels supplying the lungs. At night,

especially during the middle part, microfilariae migrate to the peripheral blood system and lymph vessels. Because of this marked 24-hour periodicity microfilariae are ingested mainly by night-biting mosquitoes such as *Anopheles*.

More than 25 anopheline species are known vectors of bancroftian filariasis. The species involved differ according to the area, and many are also the principal vectors of malaria. For example, vectors of nocturnally periodic *W. bancrofti* include *An. albimanus* (tropical Americas), *An. arabiensis*, *An. funestus*, *An. gambiae* (sub-Saharan Africa), *An. anthropophagus*, *An. balabacensis*, *An. dirus*, *An. flavirostris*, *An. letifer*, *An. leucosphyrus*, *An. maculatus*, *An. sinensis* and *An. subpictus* (India and Southeast Asia), and *An. koliensis* and *An. punctulatus* (Papua New Guinea). There are no known animal reservoir hosts of the nocturnally periodic form of filariasis.

Nocturnally periodic *B. malayi* is widespread in Asia, where it is primarily a rural disease. Transmission is by culicine mosquitoes and at least 10 anopheline species, including *An. anthropophagus*, *An. barbirostris*, *An. campestris*, *An. donaldi* and *An. sinensis*. There are no important animal reservoir hosts, although it is possible that some exist.

Brugia timori is known only from the small Indonesian islands of Alor, Timor and Flores, and from lowland areas of small neighbouring islands east of Java. Its microfilariae are nocturnally periodic and are transmitted by *An. barbirostris*, and possibly by other anopheline species. There are no known animal reservoir hosts.

Filarial development in mosquitoes

Development of all three filarial species and their mode of transmission from mosquitoes to humans are the same for all vectors. Basically, the life cycle in the mosquito is as follows. ***Microfilariae*** ingested with a blood-meal pass to the mosquito's stomach (in some vectors such as *Anopheles* many may be destroyed during their passage through the oesophagus). Within 15–30 minutes they exsheath, penetrate the stomach wall and pass into the ***haemocoel***, from where they migrate to the mosquito's ***thoracic muscles***. In the thorax the small larvae are more or less inactive, becoming shorter but considerably fatter, and after 2 days they develop into 'sausage-shaped' forms. They then undergo two moults, and the resultant ***third-stage*** larvae become active, leave the muscles and migrate through the head and down to the fleshy labium of the proboscis. This is the infective stage, and it is formed some 10 days or more after the microfilariae have been ingested with a blood-meal.

When the mosquito takes further blood-meals, several infective (third-stage) larvae (1.2–1.6 mm long) emerge from the labium and crawl onto the surface of the host's skin. However, many of these die and only a few find a skin abrasion, sometimes the small lesion caused by the

mosquito's bite, where they enter the skin and pass to the host's lymphatic system. The salivary glands are not involved in the transmission of filariasis, and there is no multiplication or sexual cycle of the parasites in the mosquito.

Infection rates of infective larvae in anopheline vectors vary according to the mosquito species and local conditions, but they are often about 0.1–5% for *W. bancrofti* and about 0.1–3% for *B. malayi*.

There are no animal reservoir hosts of *W. bancrofti*, but the nocturnally subperiodic form of *B. malayi*, transmitted by *Mansonia* mosquitoes, is a zoonosis (see Chapter 3).

The presence of filarial worms in the mosquito's thoracic muscles, or infective worms in the proboscis, does not necessarily implicate mosquitoes as vectors of bancroftian or brugian filariasis. This is because there are several other mosquito-transmitted filariae. For example, various *Setaria* species infect cattle, *Dirofilaria repens* and *D. immitis* infect dogs and humans, and other species of *Brugia*, such as *B. patei* in Africa and *B. pahangi* in Asia, infect animals but not people. Careful examination is essential to identify whether filarial parasites found in mosquitoes are those of *W. bancrofti* or *B. malayi*.

Table 3.1 (page 77) summarizes the distribution and vectors of filariasis. For information on the Global Programme to Eliminate Lymphatic Filariasis (GPELF) see Chapter 3 (page 81).

2.3.5 Arboviruses

The word arbovirus is derived from the term '***ar***thropod-***bo***rne ***virus***'. When an arbovirus is ingested by blood-sucking insects, such as mosquitoes, it can then be transmitted to human or non-human hosts and produce ***viraemia***. Within the vector the virus undergoes multiplication and/or cyclical development before being transmitted by the infected arthropod during refeeding. An arbovirus therefore undergoes obligatory development in an arthropod host. Yellow fever and dengue are typical arboviruses transmitted by *Aedes* mosquitoes. In contrast, the virus causing poliomyelitis is not an arbovirus, for although it can be transmitted by house flies this is purely mechanical transmission, that is the virus does not undergo any multiplication and/or development in an arthropod. The time taken for an infected mosquito to become ***infective*** (i.e. having virus in the salivary glands) is called the ***extrinsic incubation period***, and it varies according to temperature and the species of both arbovirus and mosquito. Over 500 arboviruses have been catalogued, but little is known about the epidemiology of many of them. About 150 arboviruses infecting humans are transmitted by mosquitoes, mostly by culicines, in particular by *Aedes* and *Culex* species. Other arboviruses are spread by other arthropods, especially ticks.

In 1959 a new painful, but non-fatal, arboviral disease called o'nyong nyong (a local African word meaning 'joint-breaker') was isolated from a patient in Uganda. In 1960–61 a major epidemic of this *Alphavirus* was identified and the disease spread to Kenya and other countries of East and Central Africa. The virus was found to be transmitted by the *An. gambiae* complex and *An. funestus*. This was the first time an *Anopheles* mosquito was incriminated as a vector of an arbovirus. Since then about 20 other arboviruses infecting humans have been found to be transmitted by *Anopheles*, none being epidemiologically very important.

2.4 Control

The principal methods of mosquito control are described in Chapter 1. Here only those methods specifically directed against *Anopheles*, mainly because of their role as malaria vectors, are considered.

2.4.1 Larval control

Formerly control of malaria vectors was based mainly on spraying larval habitats to kill *Anopheles* larvae. Where this has been properly undertaken, larvicides have reduced malaria in localized areas of economic or social importance such as principal towns, coffee and tea estates, rubber plantations and mining camps. The application of insect growth regulators (IGRs) such as pyriproxyfen and the microbial insecticide *Bacillus thuringiensis* var. *israelensis* (*Bti*) may sometimes be appropriate as a component of malaria control strategies. However, because spraying has to be repeated about every 7–14 days it is logistically impossible to control malaria over large rural areas. This only became possible with the introduction of house-spraying (see Chapter 1, page 31).

Predatory fish, mainly *Gambusia* species, continue to be used to reduce larval populations in some areas. However, they are usually not very effective in reducing malaria transmission, although they are more likely to reduce malaria in arid areas in countries such as Iran, Afghanistan, Somalia and Ethiopia, where larval habitats are discrete and permanent. In Kanarka State, India, where larvae of the malaria vector *An. culicifacies* occur in wells and ponds, introducing fish (*Poecilia reticulata*) in these habitats has significantly reduced malaria, while in Goa *An. stephensi* larvae in wells have been controlled with fish.

Draining swamps and marshes has sometimes reduced *Anopheles* populations. However, draining or filling in larval habitats is impractical in many, if not most, situations, for example with species found in temporary habitats such as scattered pools and puddles, or those occurring in forest pools and swamps.

2.4.2 Adult control

In most malaria control campaigns, control is now focused on the adults.

Indoor residual spraying (IRS)

This widely practised method consists of spraying water-dispersible (wettable) powders of residual insecticides onto the interior surfaces of walls, ceilings and roofs of houses. DDT is an effective insecticide, if vectors have not developed resistance to it. However, because DDT accumulates in mammalian tissues and residues have been found in human breast milk many countries have banned DDT. However, the presence of residues (which may be minute) does not necessarily mean that human health is affected. In 2006 both the World Health Organization (WHO) and the United States Agency for International Development (USAID) endorsed the use of DDT for spraying houses to control malaria. DDT, generally in the form of a water-dispersible powder sprayed at the rate of 2 g/m^2, is either now being used, or will soon be, in 24 countries, mostly in Africa, such as in Eritrea, Ethiopia, Mozambique, South Africa, Swaziland, Tanzania, Uganda, Zambia and Zimbabwe, and also in India, Myanmar, Papua New Guinea, Thailand and in the Americas such as in Ecuador and Venezuela. Even in highly endemic areas houses need only be sprayed at six-monthly intervals, and where malaria transmission is very seasonal, such as just during the monsoon season, a single spraying before the rains may be sufficient to give good control.

If mosquitoes are resistant to DDT then alternatives are the organophosphates such as malathion, fenitrothion or pirimiphos-methyl, the carbamates such as propoxur and bendiocarb, and pyrethroids such as lambda-cyhalothrin, deltamethrin or permethrin. However, these alternative insecticides are less persistent, and so spraying may have to be repeated every 3–4 months. These insecticides are also more expensive than DDT, but sometimes their lower dosage rates compensate for this. Most are also more toxic to people than DDT, and consequently stricter safety measures must be introduced in control programmes.

House-spraying is often popular because it also kills bedbugs, house flies and cockroaches. However, the effectiveness of house-spraying depends on mosquitoes resting indoors, whereas many important vectors, especially those in Southeast Asia and the tropical Americas, feed and/or rest out of doors. House-spraying may also promote the selection of exophilic populations of a species, that is populations that before spraying rested in houses but now rest out of doors. Similarly, spraying may reduce populations of one species of a complex that is primarily endophilic, but by so doing allow an increase in numbers of another species in the complex that is exophilic. Such population changes have been recorded in the *An. gambiae* species complex in Zimbabwe, *An. nuneztovari* in Venezuela, *An. minimus* in Thailand, and in a few other species.

Insecticide-treated nets (ITNs)

Many of the bed-nets bought by poor communities are cheap, badly made and soon tear, and torn nets are useless in protecting people against mosquito bites. Also, mosquitoes will readily bite through a net if any part of the body is pressed up against it. However, nets that are impregnated with pyrethroid insecticides such as permethrin, deltamethrin, alpha-cypermethrin and lambda-cyhalothrin will still protect people against bites even if nets are torn or people sleep up against them. Nets can be impregnated by simply dipping them in insecticide placed in a plastic bowl or dustbin. Such impregnated nets can often remain effective for 6–12 months before they need re-dipping in insecticide. Washing nets tends to make them less effective, although nets treated with some pyrethroids, such as alpha-cypermethrin, can remain effective after at least five washes. The logistics of regularly re-dipping these nets can be difficult, especially in remote areas, and it often proves unsatisfactory.

A great advance was the development of long-lasting insecticidal nets (LLINs). Their success is due to the incorporation of an insecticide into the fabric of the netting during its manufacture. There are basically two main categories of netting used in such mosquito nets. In category 1 the netting is made of polyester 75 or 100 denier multifilament yarn that has the insecticide, often deltamethrin, coating the yarn (e.g. 'PermaNets'). In category 2 the netting is made of polyethylene 100–200 denier monofilament yarn, and the insecticide, permethrin, is contained throughout the yarn (e.g. 'Olyset' nets). This results in a slow continuous release of permethrin onto the surface of the yarn. Such nets can remain effective for at least five years.

It appears that if they are used on a large scale impregnated nets can have a mass-killing effect on vector populations which can benefit the whole community, even those without nets

The recommendation of the WHO Global Malaria Programme is that only long-lasting impregnated nets (LLINs) that can withstand at least 20 washes and remain effective for at least three years of usage can give effective malaria control. However, resistance of malaria vectors, such as *An. gambiae* s.l. and *An. funestus* in East and West Africa, and the reduced susceptibility of *An. stephensi* in India, have been documented, and unfortunately such resistance is likely to increase.

Indoor residual spraying (IRS) and use of long-lasting insecticide nets (LLINs) are the two major methods currently employed to reduce malaria transmission. In some situations one of these two methods may be the most appropriate, but sometimes a combination of insecticide spraying and use of treated nets may be the best strategy.

Nets will also give variable protection against mosquito vectors of filariasis and phlebotomine sand fly vectors of leishmaniasis (Chapter 5), but will not be effective against vectors that bite out of doors or in the early evening before people have gone to bed.

2.4.3 Malaria control and malaria eradication

In 1955 the eighth World Health Assembly stated that worldwide malaria eradication, except in Africa south of the Sahara, was technically feasible. However, a sense of urgency in achieving this aim was recognized because insecticide resistance in *Anopheles* had been reported in 1950. In 1968 the 22nd World Health Assembly realized it had been over-optimistic and declared that global malaria eradication was not at present possible, although it remained the ultimate goal, and that for the time being malaria control should be the aim. It is difficult to get reliable statistics on malaria, but in 2010 it was estimated that each year more than 300 million people contracted malaria and at least 1.5 million died. About 90% of worldwide malaria deaths occur in Africa.

The difference between malaria eradication and malaria control is that eradication means the total cessation of transmission and elimination of the reservoir of infection in people so that at the end of the antimalaria campaign there is no resumption of transmission. Malaria control means reducing malaria transmission to an acceptable rate, that is to a level that no longer constitutes a major public health problem. For this, control measures have to be maintained indefinitely; if they are relaxed malaria prevalence will rise. The feasibility of control will depend not only on scientific considerations but also on the financial and public health resources of the community, or country.

The Roll Back Malaria (RBM) Partnership was launched in 1998, and is a joint initiative of WHO, UNDP, UNICEF and the World Bank, initially concentrated on Africa. Since then the partnership has expanded to incorporate non-government agencies and academic institutions, and its implementation has been extended to other parts of the world such as Asia and Latin America. It advocates an integrated approach to malaria control, involving impregnated mosquito nets, indoor house-spraying, community-level drug treatment and, if available, vaccines. The aim is that by 2015 malaria control will be an integral part of every appropriate development activity and the achievements will be maintained. However, in October 2007 the Melinda and Bill Gates Foundation declared that malaria eradication was feasible, which surprised many malaria experts, although some believed it might just be possible. See Das & Horton (2010) for a discussion on the feasibility of malaria eradication.

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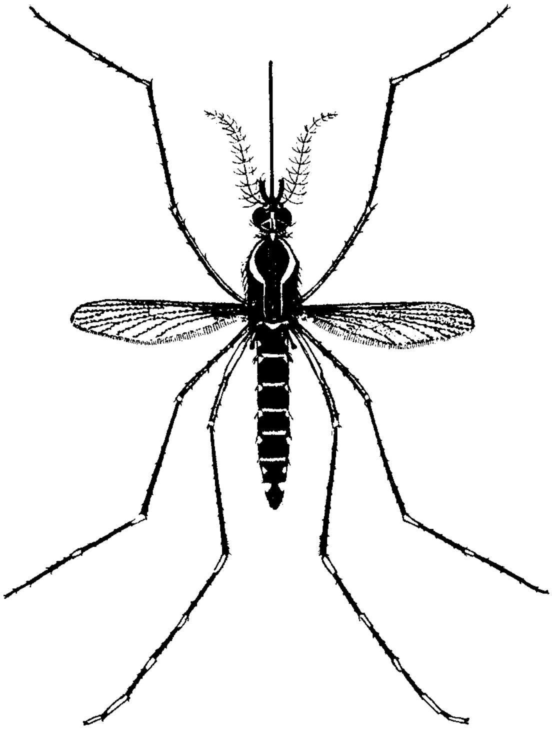
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See also references at the ends of Chapters 1 and 3.

3

Culicine mosquitoes (Culicinae)



Conservatively the subfamily Culicinae contains 40 genera, but as already mentioned (see Chapter 1) some taxonomists recognize many more genera, two of which are *Stegomyia* and *Ochlerotatus*, resulting in two medically important species being named *Stegomyia aegypti* and *Ochlerotatus albopictus*. However, in this book all species attributed to these two new genera are retained in the genus *Aedes*, such as *Aedes aegypti* and *Aedes albopictus*, with *Stegomyia* and *Ochlerotatus* recognized as subgenera.

The medically most important genera are *Culex*, *Aedes*, *Haemagogus*, *Sabethes* and *Mansonia*, while *Coquillettidia* and *Psorophora* are of lesser importance. Species of *Culex*, *Aedes* and *Coquillettidia* are found in both temperate and tropical regions, whereas *Psorophora* species occur only in North, Central and South America. *Haemagogus* and *Sabethes* mosquitoes are restricted to Central and South America. *Mansonia* occurs mainly in the tropics.

Certain *Aedes* mosquitoes are vectors of yellow fever in Africa, and *Aedes*, *Haemagogus* and *Sabethes* are yellow fever vectors in Central and South America. *Aedes* species are also vectors of the classical and haemorrhagic forms of dengue. All seven genera of culicine mosquitoes mentioned here, as well as some others, can transmit a variety of other arboviruses. Some *Culex*, *Aedes* and *Mansonia* species are important vectors of filariasis (*Wuchereria bancrofti* or *Brugia malayi*). *Psorophora* species are mainly pest mosquitoes but a few transmit arboviruses, while *Coquillettidia crassipes* can also be a vector of brugian filariasis.

Characters separating the subfamily Culicinae from the Anophelinae have been outlined in Chapter 1 and are summarized in Table 1.1 (page 18).

It is not easy to give a reliable and non-technical guide to the identification of the most important culicine genera. Nevertheless, characters that will usually separate these genera are given below, together with notes on their biology.

3.1 *Culex* mosquitoes

3.1.1 Distribution

Culex mosquitoes are found more or less worldwide, but they are absent from the extreme northern parts of the temperate zones.

3.1.2 Eggs

Eggs are usually brown, long and cylindrical, laid upright on the water surface and placed together to form an ***egg raft*** which can comprise up to about 300 eggs (Fig. 1.15). No glue or cement-like substance binds the eggs to each other; adhesion is due to surface forces holding the eggs together. A few other mosquitoes, including those of the genus *Coquillettidia*, also deposit their eggs in rafts.

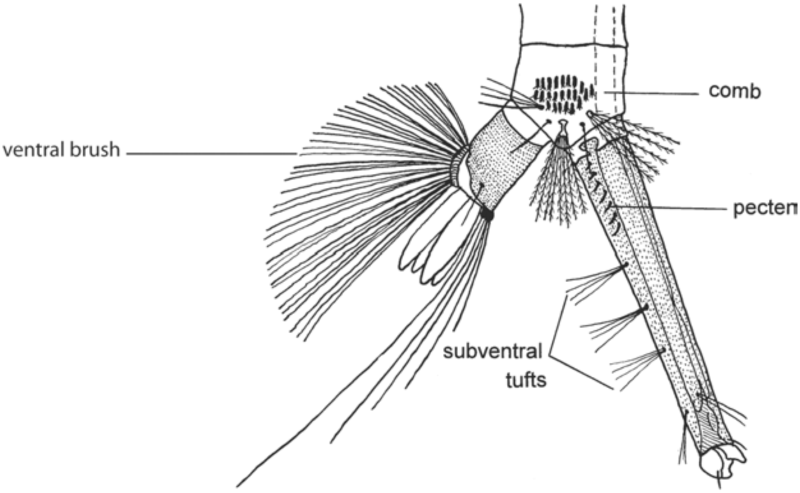


Figure 3.1 Terminal abdominal segments of a *Culex* larva, showing the long siphon with more than one (three shown here) subventral tufts of hair.

3.1.3 Larvae

The larval siphon is often long and narrow (Fig. 3.1), but it may be short and fat. There is always ***more than one pair*** of ***subventral tufts*** of hairs on the siphon, none of which is near the base. These hair tufts may consist of very few short and simple hairs, which can be missed unless larvae are carefully examined under a microscope.

3.1.4 Adults

Frequently, but not always, the thorax, legs and wing veins of the adult are covered with ***dull-coloured***, often brown, scales (Plate 2). The abdomen is often covered with brown or blackish scales, but some whitish scales may occur on most segments. Adults are recognized more by their lack of ornamentation than by any striking diagnostic characters. The tip of the female abdomen is not pointed but ***blunt***. Claws on all tarsi are simple and those on the hind tarsi are very small. Examination under a microscope shows that all tarsi have a pair of small fleshy ***pulvilli*** (Fig. 1.2).

3.1.5 Biology

Eggs are laid in a great variety of aquatic habitats. Larval habitats of most *Culex* species are ***ground collections*** of water such as pools, puddles, ditches, borrow pits and ricefields. Some species lay their eggs in man-made container-habitats such as tin cans, water receptacles, bottles and water-storage tanks. Only a few species are found in tree-holes and even fewer in leaf axils. Larvae of the medically most important species, *Culex*

quinquefasciatus, which is a vector of bancroftian filariasis, occur in waters polluted with organic debris such as rotting vegetation, household refuse and excreta. Larvae are also commonly found in partially blocked drains and ditches, soakaway pits and septic tanks, and in village pots, especially abandoned ones in which water is polluted and unfit for drinking. It is a mosquito that is associated with urbanization, especially towns with poor and inadequate drainage and sanitation. Under these conditions its population increases rapidly. Adults mainly bite at night.

Culex quinquefasciatus, and many other *Culex* species, bite humans and other hosts ***at night***. Some species, such as *Cx. quinquefasciatus*, commonly rest indoors both before and after feeding, but they also shelter in outdoor resting places.

Culex tritaeniorhynchus is an important vector of Japanese encephalitis and breeds in ricefields and grassy pools. In southern Asia larvae are sometimes found in fish ponds which have had manure added to them.

3.2 *Aedes* mosquitoes

3.2.1 Distribution

Worldwide, the geographical range of *Aedes* mosquitoes extends well into northern and arctic areas, where they can be vicious biters and serious pests to both people and livestock.

3.2.2 Eggs

Eggs are usually black, more or less ovoid in shape, and are always laid ***singly*** (Fig. 1.15). Careful examination shows that the eggshell has a distinctive mosaic pattern. Eggs are laid on damp substrates just beyond the water line, such as on damp mud and leaf litter of pools, on the damp surfaces of clay pots, rock-pools and tree-holes.

Eggs can withstand ***desiccation***, the intensity and duration of which varies, but in many species they can remain dry but viable for many months or occasionally a year or more. When flooded, some eggs may hatch within a few minutes, while others of the same batch may require longer immersion in water before they hatch, and consequently hatching may be spread over several days or weeks. Even when eggs are soaked for long periods some may fail to hatch because they require several soakings followed by short periods of desiccation before hatching can be induced. Even if environmental conditions are favourable, eggs may be in a state of ***diapause*** and will not hatch until this resting period is terminated. Various stimuli, including reduction in the oxygen content of water, changes in day length, and temperature, may be required to break diapause in *Aedes* eggs.

Larvae of many *Aedes* species occur in small ***container-habitats*** (tree-holes, plant axils, etc.) which are susceptible to drying out; thus the ability

of eggs to withstand ***desiccation*** is clearly advantageous. Desiccation and the ability of eggs to hatch in instalments can create problems with controlling the immature stages (see page 79).

3.2.3 Larvae

Aedes species usually have a short barrel-shaped siphon, and there is only ***one pair*** of ***subventral tufts***, which arises about one-quarter or more from the base of the siphon (Fig. 3.2). There are at least three pairs of setae in the ventral brush. The antennae are not greatly flattened and there are no very large setae on the thorax. These characters should separate *Aedes* larvae from most of the culicine genera, but not unfortunately from larvae of South American *Haemagogus*. In Central and South America *Aedes* larvae can usually be distinguished from those of *Haemagogus* by possessing either larger or more strongly spiculate antennae and the comb (Fig. 3.2) not being on a sclerotized plate as in some *Haemagogus*.

3.2.4 Adults

Many, but not all, *Aedes* adults have conspicuous ***patterns*** on the thorax formed by black, white or silvery scales (Fig. 3.3, Plate 3), and in some species yellow and/or brownish scales are present. The legs often have dark and white rings (Fig. 3.4b). *Aedes aegypti*, often called the yellow fever mosquito, is readily recognized by the lyre-shaped silver markings on the lateral edges of the scutum (Fig. 3.3b). Scales on the wing veins of

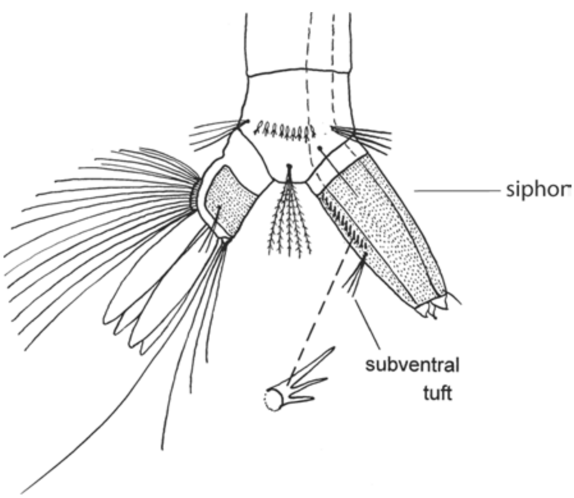
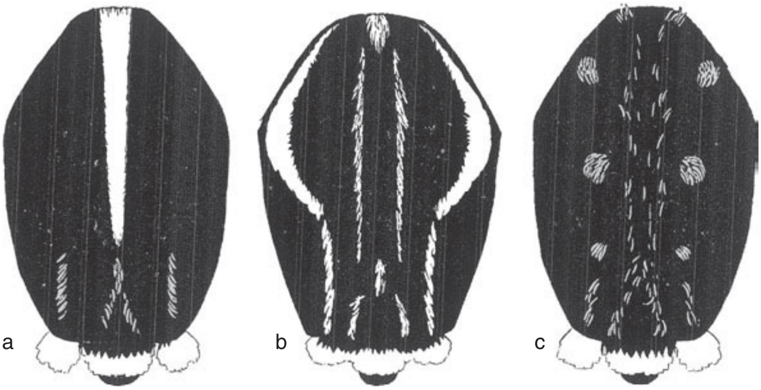
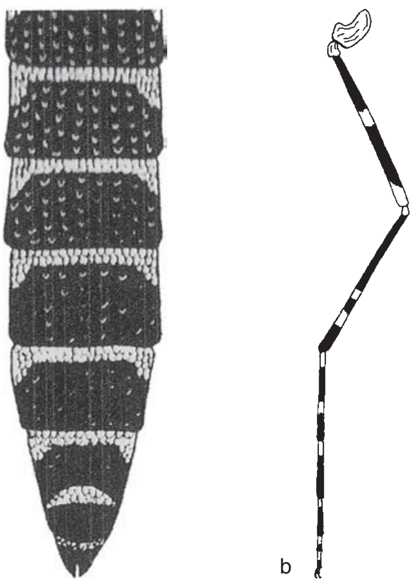


Figure 3.2 Terminal abdominal segments of an *Aedes* larva, showing the short siphon with a single subventral hair tuft.



a b c

Figure 3.3 Dorsal surfaces of the thoraces of adult *Aedes* mosquitoes, showing examples of thoracic patterns of dark and pale scales: (a) *Ae. albopictus*, with a diagnostic median white stripe; (b) *Ae. aegypti*, with black scales and typical lyre-shaped silvery markings; (c) *Ae. vittatus*, with six rather indistinct lateral white spots.



a b

Figure 3.4 (a) Abdomen and (b) leg of an *Aedes* adult, showing typical arrangement of black and white scales.

Aedes mosquitoes are narrow and usually mainly black. In *Aedes* the abdomen is often covered with black and white scales forming distinctive patterns, and in the female the abdomen is pointed at its tip (Fig. 3.4a).

3.2.5 Biology

Although the larval habitats of some *Aedes* species are marshes and ground pools, including snow-melt pools in arctic and subarctic areas, many, especially tropical species, are found in natural ***container-habitats*** such as tree-holes, bamboo stumps, leaf axils and rock-pools, or in man-made ones such as water-storage pots, tin cans and tyres. For example, *Ae. aegypti* larvae commonly occur in water-storage pots or jars that are either inside or outside houses. Larvae occur mainly in pots having clean water intended for drinking. In some areas *Ae. aegypti* larvae are also found in rock-pools and tree-holes. *Aedes africanus*, an African species involved in the sylvatic transmission of yellow fever, breeds mainly in tree-holes and bamboo stumps, whereas *Ae. bromeliae*, another African yellow fever vector, breeds almost exclusively in leaf axils, especially those of banana plants, pineapples and coco-yams (*Colocasia* species).

Aedes albopictus (Fig. 3.3a), a vector of dengue in Southeast Asia, breeds in both natural and man-made container-habitats such as tree-holes, water-storage pots and vehicle tyres. This species was introduced into the continental USA in 1985 as dry, but viable, eggs that had been oviposited in tyres in Asia which were then exported. It can also be introduced into countries by eggs in lucky bamboo (*Dracaena* species), in which there is an increasing trade. By 2010 *Ae. albopictus* had spread to more than 29 states in the USA. It is found in many Latin American countries, in some sub-Saharan African countries, in 15 European countries, in Israel and in both Australia and New Zealand. In summary, it has been reported from more than 27 countries outside Asia. However, *Ae. albopictus* has often failed to become established in many countries having a more temperate climate or where efficient control has rapidly eliminated invasions.

Larvae of *Ae. polynesiensis* occur in both man-made and natural container-habitats, especially split coconut shells in Polynesia, whereas larvae of *Ae. pseudoscutellaris* are found in tree-holes and bamboo stumps in Fiji. Both species are important vectors of diurnally subperiodic bancroftian filariasis. *Aedes togoi*, which is a minor vector of nocturnally periodic bancroftian and brugian filariasis in China, breeds principally in rock-pools containing fresh or brackish water.

The life cycle of *Aedes* mosquitoes from eggs to adults can be rapid, taking as little as seven days, but is usually 10–12 days; in temperate species the life cycle may last several weeks to many months,and some species overwinter as eggs or larvae.

Adults of most *Aedes* species bite mainly during the ***day*** or early evening. Most biting occurs out of doors and adults usually rest out of doors before and after feeding.

3.3 *Haemagogus* mosquitoes

3.3.1 Distribution

Haemagogus mosquitoes are found only in Central and South America.

3.3.2 Eggs

Eggs are usually black and ovoid and laid singly in tree-holes and other natural container-habitats, and occasionally in man-made ones. There is no simple method of distinguishing eggs of *Haemagogus* from those of *Aedes* or *Psorophora* mosquitoes.

3.3.3 Larvae

Larvae have only one pair of subventral tufts arising, as in *Aedes* species, one-quarter or more from the base of the siphon. They resemble *Aedes* larvae but can usually be distinguished by the antennae being short and either lacking spicules or having only a very few, and by the ventral brush arising from a sclerotized ***boss*** (Fig. 3.5). In some species the comb teeth are arranged at the edge of a sclerotized ***plate;*** in *Aedes* this plate is absent.

3.3.4 Adults

Adults are very ***colourful*** and can easily be recognized by having broad, flat and bright metallic blue, red, green or golden scales covering the dorsal

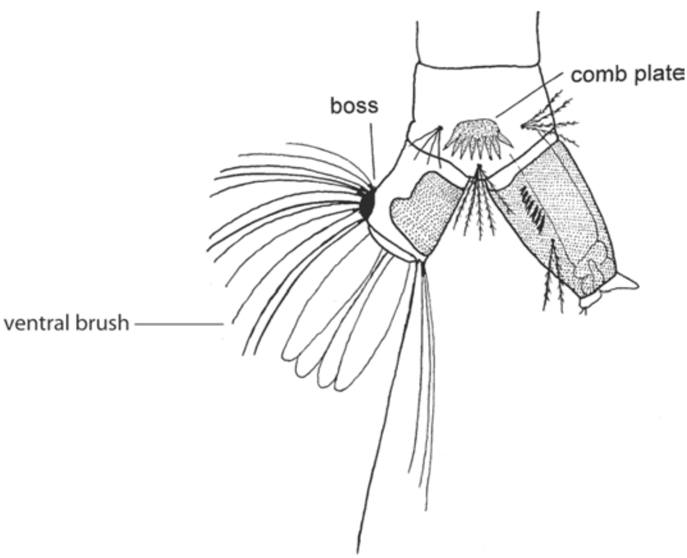


Figure 3.5 Terminal abdominal segments of a *Haemagogus* larva, showing a ventral brush arising from a dark sclerotized boss, and comb scales arranged on a small 'plate'.

part of the thorax. Like *Sabethes* mosquitoes (Fig. 3.7a), they have exceptionally large ***antepronotal thoracic lobes*** behind the head. *Haemagogus* adults are rather similar to those of *Sabethes*, and it may be difficult for the novice to separate these two genera. However, no *Haemagogus* mosquito has paddles on the legs, which is a conspicuous feature of many, but not all, *Sabethes* species (Fig. 3.7c).

3.3.5 Biology

Eggs can withstand ***desiccation***. Larvae occur mostly in tree-holes and bamboo stumps, but also in rock-pools, split coconut shells and sometimes in assorted domestic containers. They are basically ***forest mosquitoes***. Adults bite during the day and mostly in the tree-tops, where they feed on monkeys. However, under certain environmental conditions such as experienced at the edges of forests during tree-felling operations or during the dry season, adults may descend to the forest floor to bite humans and other hosts. Species such as *Haemagogus spegazzinii*, *Hg. leucocelaenus* and *Hg. janthinomys* are all involved in yellow fever transmission in forests.

3.4 *Sabethes* mosquitoes

3.4.1 Distribution

Sabethes mosquitoes are found only in Central and South America.

3.4.2 Eggs

Little is known about the eggs of *Sabethes* species, but they are laid singly, have no prominent surface features such as bosses or sculpturing and are incapable of withstanding desiccation. Eggs of *Sabethes chloropterus*, a species sometimes involved in the sylvatic cycle of yellow fever, are rhomboid in shape and can thus be readily distinguished from most other culicine eggs (Fig. 3.7b).

3.4.3 Larvae

The larval siphon is relatively slender and moderately long (Fig. 3.6) and has many ***single*** hairs placed ventrally, laterally or dorsally. *Sabethes* larvae can usually be distinguished from other mosquito larvae by having only ***one pair*** of setae in the ventral brush, the comb teeth arranged in a single row, or at most with three or four detached teeth, and by the absence of a pecten.

3.4.4 Adults

The dorsal surface of the thorax is covered with appressed ***iridescent*** blue, green and red scales (Plate 4). The ***antepronotal lobes***, like those in

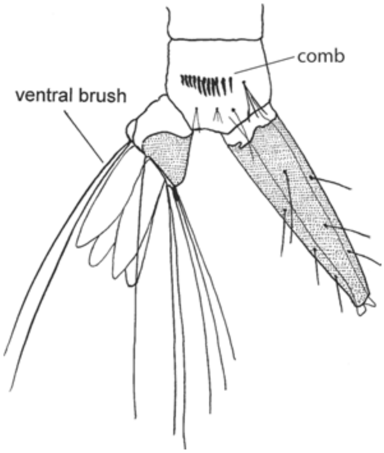


Figure 3.6 Terminal abdominal segments of a *Sabethes* larva, showing a single pair of hairs in the ventral brush, the comb, numerous single hairs on the siphon, and absence of a pecten on the siphon.

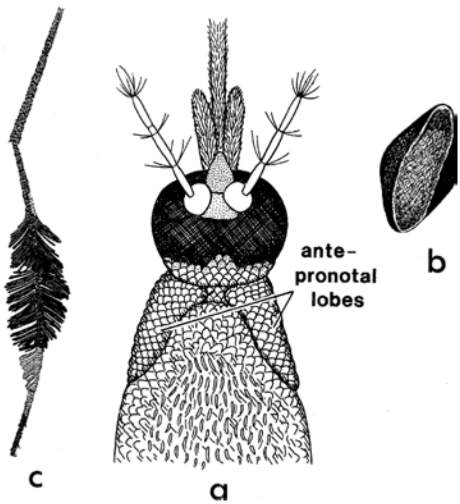


Figure 3.7 *Sabethes* mosquitoes: (a) head and thorax, showing antepronotal lobes forming a 'collar' behind the head; (b) an egg; (c) hindleg, showing long narrow scales forming a 'paddle'.

Haemagogus, are very large (Fig. 3.7a). Adults of many species have one or more pairs of tarsi with conspicuous ***paddles*** composed of narrow scales (Fig. 3.7c). Their presence immediately distinguishes *Sabethes* from all other mosquitoes. Species which lack these paddles resemble those of *Haemagogus*, and a specialist is required to identify them.

3.4.5 Biology

Larvae occur in tree-holes and bamboo stumps, but a few species are found in leaf axils of bromeliads and other plants. They are ***forest mosquitoes***. Adults bite during the day and mainly in the tree canopy, but like *Haemagogus* adults may descend to ground level at certain times to bite humans and other hosts. *Sabethes chloropterus* has been incriminated as a sylvan vector of yellow fever.

3.5 *Mansonia* mosquitoes

3.5.1 Distribution

Mansonia is principally a genus of wet tropical areas, but a very few species occur in temperate regions.

3.5.2 Eggs

Eggs are dark brown or blackish and cylindrical, but have a tube-like extension apically which is usually darker than the rest of the egg (Fig. 3.8). Eggs are laid in sticky compact ***masses***, often arranged as a rosette, which are glued to the undersurface of floating vegetation (Figs. 1.15, 3.8).

3.5.3 Larvae

Mansonia larvae are easily recognized because they have a ***specialized siphon*** adapted for piercing aquatic plants to obtain air (Fig. 3.9b,c). The siphon tends to be conical, with the apical part darker and heavily sclerotized, and it has teeth and curved hairs which assist a larva to attach itself to plants and insert its siphon. The pupal respiratory trumpets are also inserted into plants for respiration (Fig. 3.9a).

3.5.4 Adults

Typically adults have the legs (Fig. 3.10c), palps, wings and body covered with a ***mixture*** of dark (usually brown) and pale (usually white or creamy) scales, giving the mosquito a rather dusty appearance. The scattering of dark and pale scales on the wing veins gives the wings the appearance of having

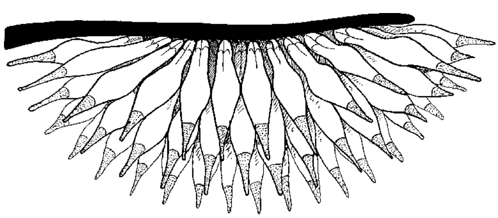


Figure 3.8 *Mansonia* eggs glued to the underside of floating aquatic vegetation.

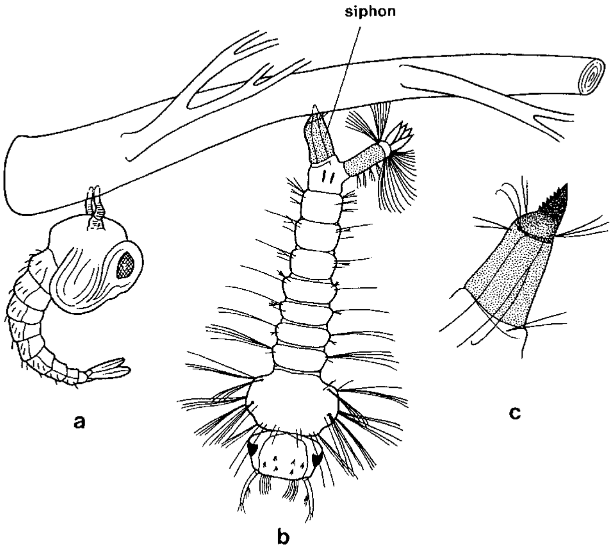


Figure 3.9 Immature stages of *Mansonia* mosquitoes: (a) pupa with respiratory trumpets inserted into an aquatic plant; (b) larva with siphon inserted into an aquatic plant for respiration; (c) larval siphon, showing serrated structures used to pierce aquatic plants.

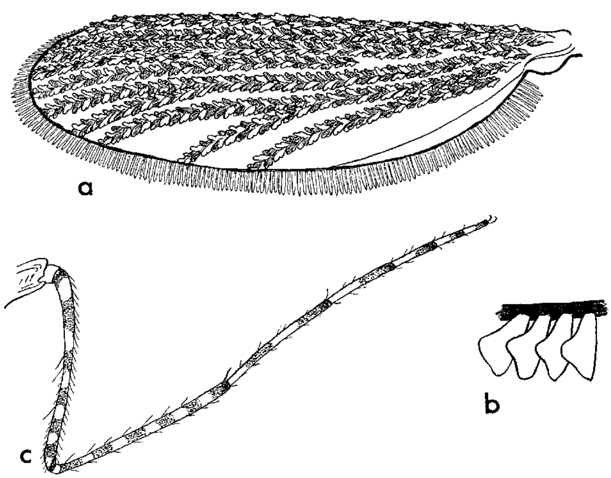


Figure 3.10 *Mansonia* mosquitoes: (a) wing, showing speckled distribution of dark and pale scales; (b) a few scales on a wing vein, showing their broad, almost heart shape; (c) leg, showing distribution of dark and pale scales giving a banded pattern.

been sprinkled with salt and pepper (Fig. 3.10a), and provides a useful character for identification. Closer examination shows that the scales on the wings are very broad and often asymmetrical and almost ***heart-shaped*** (Fig. 3.10b). In other mosquitoes these scales are longer and narrower.

3.5.5 Biology

Eggs are glued to the undersurface of plants and hatch within a few days; they are unable to withstand desiccation. All larval habitats have aquatic vegetation, either rooted (such as grasses, rushes and reeds) or floating (such as *Pistia stratiotes*, *Salvinia* or *Eichhornia* species). Larvae consequently occur in permanent collections of water such as swamps, marshes, ponds, borrow pits, grassy ditches, irrigation canals and even in the middle of rivers if they have floating plants.

Larvae and pupae only detach themselves from plants and rise to the water surface if they are disturbed. Because they are more or less permanently attached to plants the immature stages are frequently missed in larval surveys. It is therefore not easy to identify breeding places unless special collecting procedures are undertaken, such as removing plants and examining them for attached *Mansonia* larvae and pupae. Because it is difficult to get insecticides to the larvae, which may be some distance below the water surface, it is often difficult to control *Mansonia* mosquitoes with conventional insecticidal applications. However, herbicides can be used to kill the plants on which larvae are attached (see page 81).

Adults usually bite at night, but a few species are day-biters. After feeding, most *Mansonia* rest out of doors, but a few species rest indoors. The main medical importance of *Mansonia* mosquitoes is as vectors of filariasis, such as the nocturnally periodic and nocturnally subperiodic forms of *Brugia malayi* in Asia. In Africa filariasis (*W. bancrofti*) is not transmitted by *Mansonia* species, although they can be vectors of a few, but not very important, arboviruses.

3.6 *Coquillettidia* mosquitoes

The genus *Coquillettidia* is of lesser medical importance and is therefore described only briefly. It is mainly tropical, but a few species occur in temperate regions. *Coquillettidia* is related to *Mansonia* and has sometimes been treated as a subgenus of *Mansonia*, but species of *Coquillettidia* differ in several respects. For example, as in *Culex* species, eggs are formed into ***egg rafts*** that float on the water, but they are narrower and longer than *Culex* rafts. Larvae have rather conical siphons, which like those of *Mansonia* are inserted into plants for respiratory purposes, but the larval antennae are much longer than those in *Mansonia*. Adults have narrow scales on the wings, not broad or heart-shaped ones as found in *Mansonia*, and several *Coquillettidia* species are a bright ***yellow***. *Coquillettidia crassipes* can be a vector of nocturnally subperiodic *B. malayi* in Southeast Asia.

3.7 *Psorophora* mosquitoes

Psorophora mosquitoes are of little medical importance and so are described briefly. They are found from Canada to South America. They are similar in

many respects to *Aedes* species: for example, their eggs look like *Aedes* eggs and like them they can withstand ***desiccation***. Adults of some pest species are large mosquitoes. A specialist is required to distinguish the larvae from those of *Aedes* species. Larval habitats are mainly flooded pastures and sometimes ricefields; larvae of several species are predators. Although adults can be vectors of a few arboviruses, such as Venezuelan equine encephalitis, their main importance is as vicious biting pests.

3.8 Medical importance

3.8.1 Biting nuisance

In some cases, a considerable amount of money is spent on mosquito control not because they are vectors of disease but because they are troublesome biters. For example, some of the best-organized mosquito control operations are in North America, where large amounts of money may be spent on mosquito control, often more than in some tropical countries where mosquitoes are important vectors of diseases such as malaria. However, in northern temperate and subarctic areas of America, Europe and Asia much greater numbers of mosquitoes can be encountered biting people than in tropical countries. Although they may not be transmitting diseases to humans in these areas they can, nevertheless, make life outdoors intolerable.

3.8.2 Arboviruses

Numerous arboviruses are transmitted by culicine mosquitoes, including important ones such as those causing yellow fever and dengue. *Aedes* and *Culex* species are the most important vectors of arboviruses.

The intrinsic incubation period of a virus in humans is usually just a few days, often 3–4 days, after which virus appears in the peripheral blood and the host is viraemic. ***Viraemia*** lasts only a few days, typically 3 days, after which the virus disappears from the peripheral blood. A vector must bite a viraemic host if it is to become infected and transmit an infection.

A relatively high titre of arbovirus is usually required before a virus can pass across the gut wall of the mosquito into the haemolymph. From the haemolymph the virus invades many tissues and organs, including the ***salivary glands***, where virus multiplication occurs. This is the ***extrinsic incubation period*** of development and can take 5–30 days, depending on temperature, the type of virus and the mosquito species. In most mosquito-borne viral infections the extrinsic cycle is typically 8–15 days.

3.8.3 Yellow fever (*Flavivirus*)

The arbovirus causing yellow fever occurs in Africa and tropical areas of the Americas. It does not occur in Asia or elsewhere, although mosquitoes

capable of transmitting the disease occur in many countries. Yellow fever is a ***zoonosis***, being essentially an infection of forest monkeys which under certain conditions can be transmitted to humans. The World Health Organization (WHO) estimates that there are 200 000 cases and 30 000 deaths a year caused by yellow fever.

Africa

About 90% of yellow fever cases occur in Africa, where it is endemic in 33 countries. Outbreaks of yellow fever occurred in 2010 in the Ivory Coast, Guinea, Cameroon, the Democratic Republic of the Congo and Senegal; in 2009 in the Central African Republic, Cameroon, Liberia, the Republic of the Congo, Guinea and Sierra Leone. In 2008 yellow fever was recorded in five West African countries, in 2007 just in Togo, but in 2006 it occurred in six West African countries. Other outbreaks had occurred prior to 2006, showing that yellow fever in West Africa is a perpetual problem.

In Africa the yellow fever virus occurs in certain cercopithecid monkeys (e.g *Colobus* and *Cercopithecus* species) inhabiting the forests. Other primates also act as reservoir hosts, and in East Africa the lesser bushbaby (*Galago senegalensis*) is an important host. The virus is transmitted amongst these primates by tree-hole-breeding mosquitoes, mainly *Aedes africanus*. This forest-dwelling mosquito bites mainly in the forest canopy soon after sunset – just in the right place and at the right time to bite monkeys going to sleep in the tree-tops. This ***sylvatic cycle***, or savanna, forest or monkey cycle as it is sometimes called, maintains a virus reservoir in the monkey population (Fig. 3.11). In Africa, monkeys are little affected by yellow fever, dying only occasionally, although in East Africa infected bushbabies (*Galago* species) usually die. Some of the monkeys involved in the forest cycle descend from the trees to steal bananas from farms at the edge of the forest. In this habitat the monkeys get bitten by different mosquitoes, for example by *Aedes bromeliae* (formerly called *Ae. simpsoni*), a species that breeds in leaf axils of bananas, plantains, coco-yams (*Colocasia* species) and pineapples, and in West Africa also by other species such as tree-hole-breeding *Aedes furcifer*, *Ae. opok* and *Ae. luteocephalus*. These species bite during the day at the edges of forests, and if the monkeys have viraemia, that is yellow fever virus circulating in their peripheral blood, the mosquitoes become infected. If these mosquitoes live sufficiently long they can transmit yellow fever to other monkeys, or more importantly to people. This transmission cycle, occurring in clearings at the edge of forests involving both monkeys and humans, is sometimes referred to as the ***rural cycle*** (Fig. 3.11). When people return to their villages, or travel to towns, they get bitten by different mosquitoes, including *Ae. aegypti*, a domestic species breeding mainly in man-made containers such as water-storage pots, abandoned tin cans and vehicle tyres. If people have viraemia then *Ae. aegypti*

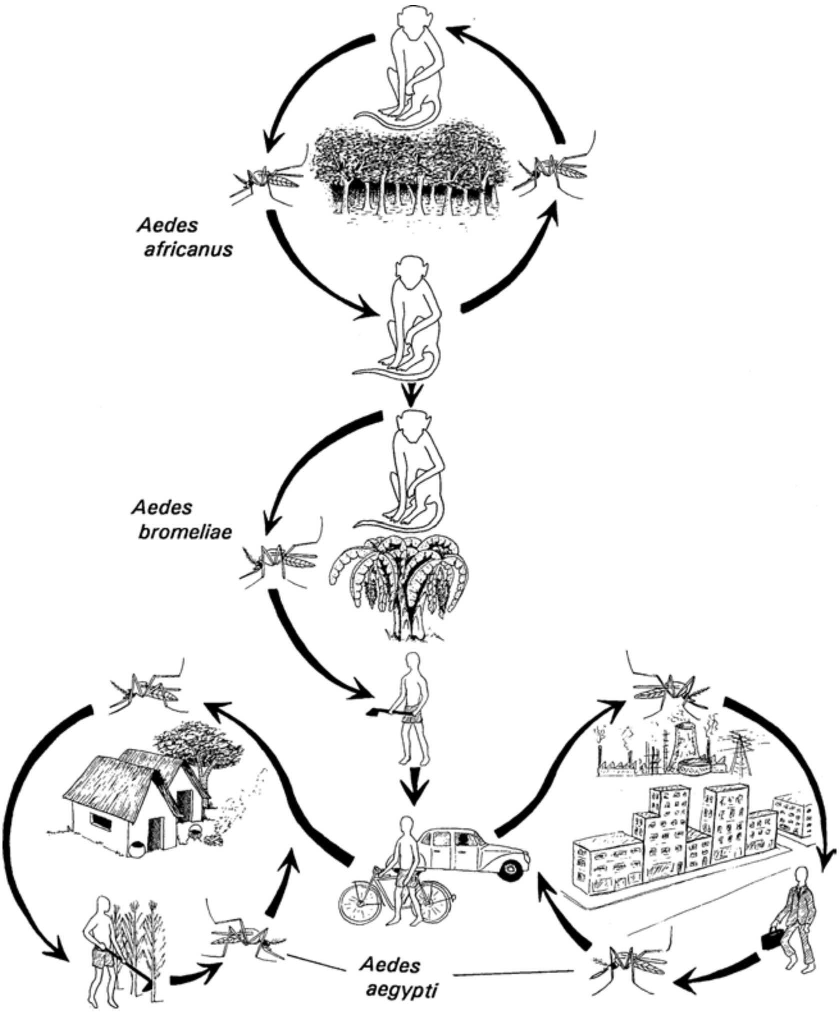


Figure 3.11 Diagrammatic representation of the sylvatic, rural and urban cycles of yellow fever transmission in Africa (only major vectors included).

becomes infected and yellow fever is transmitted among the human population by this species. This is the ***urban cycle*** of yellow fever transmission (Fig. 3.11).

The epidemiology of yellow fever is complicated and variable. In some areas, for example, yellow fever may be circulating among the monkey population yet rarely gets transmitted to humans because local vector mosquitoes are predominantly zoophagic. Compared to West Africa, outbreaks of yellow fever in East Africa are, for some reason, much less common.

Yellow fever virus may be ***transovarially*** transmitted in *Aedes* species. That is, eggs and subsequent generations arising from infected adults are born already infected with the virus. (Transovarial transmission is more usually associated with tick-borne diseases than with mosquitoes.) The virus can also be passed from congenitally infected males to females during mating, which in effect is venereal transmission. How important these routes of infection are remains unclear, but such mechanisms, especially transovarial transmission, would provide a means of virus survival during long dry seasons.

Americas

In Central and South Americas yellow fever is endemic in 11 countries. Outbreaks of yellow fever occurred in 2008 in Paraguay and Brazil, in 2007–2008 in Argentina, in 2004 in Venezuela, in 2003 in Brazil, in 2001 in Peru and Brazil and in 2000 again in Brazil. It is clear that yellow fever is not as great a problem in the Americas as in West Africa (see page 68).

In Central and South America the yellow fever cycle, although similar to that in Africa, differs in certain aspects (Fig. 3.12). As in Africa, it is an infection of forest monkeys, mainly cebid ones (e.g. howler monkeys (*Alouatta* species), squirrel monkeys (*Saimiri* species) and spider monkeys (*Ateles* species)), and it is transmitted among them by forest-dwelling mosquitoes. In the ***sylvatic*** or ***jungle cycle*** the vectors are *Haemagogus* species including *Hg. spegazzinii*, *Hg. leucocelaenus* and *Hg. janthinomys* and to a lesser extent *Sabethes chloropterus*, and sometimes also *Aedes* species. These are all arboreal mosquitoes which bite in the forest canopy and breed in tree-holes or bamboo. New World monkeys are more susceptible to yellow fever than African monkeys and frequently become sick and die. When people enter the jungle to cut down trees for timber, mosquitoes which normally bite monkeys at canopy heights may descend and bite them; if these mosquitoes are infected, people will develop yellow fever. The disease is then spread from person to person in villages and towns, as in Africa, by *Ae. aegypti* (Fig. 3.12), and this constitutes the ***urban cycle***. However, no urban cases had been recorded in South America since 1942 – that is, until the outbreak in Paraguay in 2008.

Transovarial transmission has been reported in *Haemagogus* species.

3.8.4 Dengue (*Flavivirus*)

Dengue is the most rapidly spreading mosquito-borne viral infection in the world. An estimated 50 million dengue infections occur annually, and some 2.5 billion people live in more than 100 countries in which it is endemic. Dengue is now endemic in all WHO regions except the European Region.

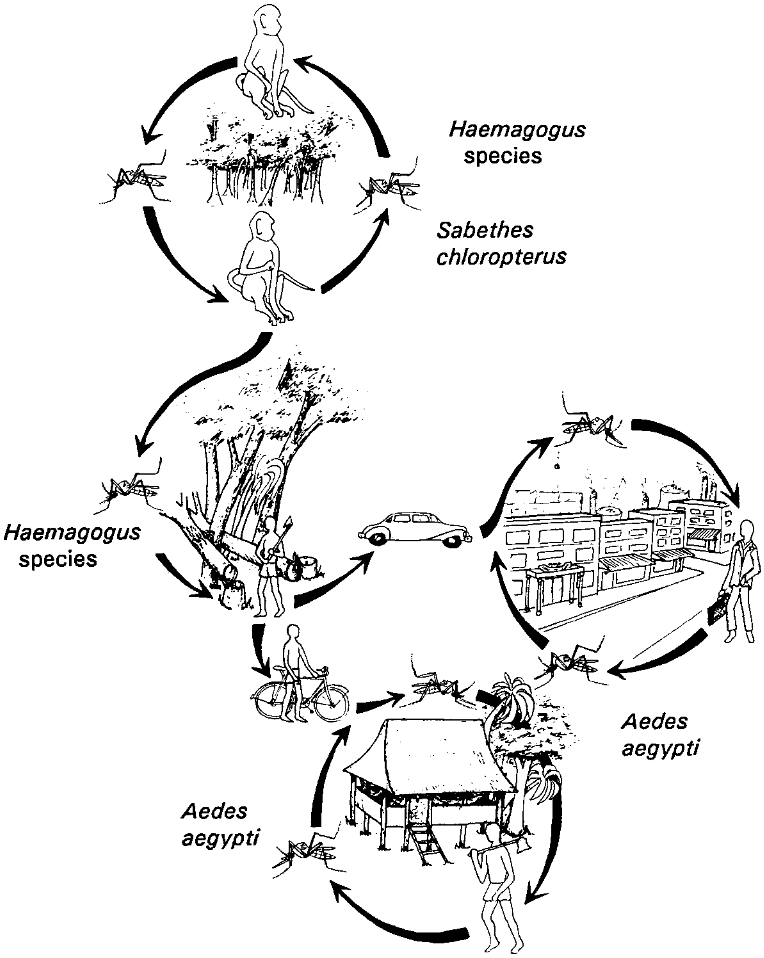


Figure 3.12 Diagrammatic representation of the jungle, rural and urban cycles of yellow fever transmission in Central and South America.

Dengue is caused by four similar viruses (DENV-1, -2, -3 and -4) and is endemic throughout most of Southeast Asia, the Pacific Region, the Indian subcontinent, sub-Saharan Africa, Central and South America and the Caribbean. In September 2009 dengue was transmitted in Key West, Florida, USA, and this was the first time dengue occurred in Florida since 1934.

Dengue haemorrhagic fever is a potentially lethal complication causing infant mortality, and it has appeared in many parts of Southeast Asia and India. In 1981 haemorrhagic dengue and dengue type 4 were first noticed in Cuba. In 2007 Venezuela had over 80 000 cases, of which 6000 were haemorrhagic dengue, while in Brazil there were over 77 000 cases and at

least 70 deaths in Rio de Janeiro in the first 6 months of 2011, which is more than the combined total of cases in 2009 and 2010. Both dengue and haemorrhagic dengue are transmitted by *Ae. aegypti* and to a lesser extent by *Ae. albopictus*; both species breed in natural and man-made container-habitats such as water-storage pots and tyres. Transovarial transmission has been reported in *Ae. aegypti* and *Ae. albopictus*. Mosquitoes of the *Ae. scutellaris* group, which also breed in natural and man-made containers, can also be vectors in some parts of the Western Pacific area. Although transmission of dengue virus amongst monkeys in forests of Sri Lanka, Malaysia, Vietnam and West Africa has been reported, there is little evidence that enzootic strains are involved in epidemics. Transmission is among the human population, and humans are the reservoir hosts. As yet there is no vaccine.

3.8.5 West Nile virus (WNV) (*Flavivirus*)

West Nile virus is a member of the Japanese encephalitis group. The virus was first isolated in 1937 from a febrile patient in Uganda. The virus has now spread to the Middle East, many African countries and about 24 European countries where there are usually only a few cases of WNV a year. However, in 2010 there were at least 173 cases and 15 deaths in Greece. In 1999 the virus was recorded for the first time from the Americas, in New York State. How the virus entered North America is unresolved, but it seems likely due to infective migrant birds. West Nile virus has been recorded from 48 states in the continental USA and in six Canadian provinces. The virus has also spread to Mexico and several countries in Central America, South America and the Caribbean.

The virus is principally an infection of birds. Crows (*Corvus* species) are the commonest birds in the USA to be found dead and infected with WNV, but many other bird species are infected, and laboratory experiments show some to be potentially more efficient hosts than crows. Virus has been isolated from more than 75 mosquito species, although *Culex* mosquitoes, such as *Cx. pipiens*, *Cx. quinquefasciatus* and *Cx. tarsalis* in the USA, and *Cx. pipiens*, *Cx. torrentium* and *Cx. modestus* in Europe, are among the most important vectors. (It has been shown that there can be co-feeding transmission: that is when an uninfected mosquito is feeding on a host very near an infected mosquito the virus from the infected mosquito can pass to the uninfected mosquito, thus making it a potential vector.) Occasionally a mosquito species that feeds on both birds and mammals, a so-called ***bridge vector***, transfers the infection to humans, horses and other mammals. Mammals are incidental hosts and are termed ***dead-end hosts*** because mosquitoes feeding on infected mammals cannot pick up sufficient virus to infect further mammals when they bite them (Fig. 3.13).

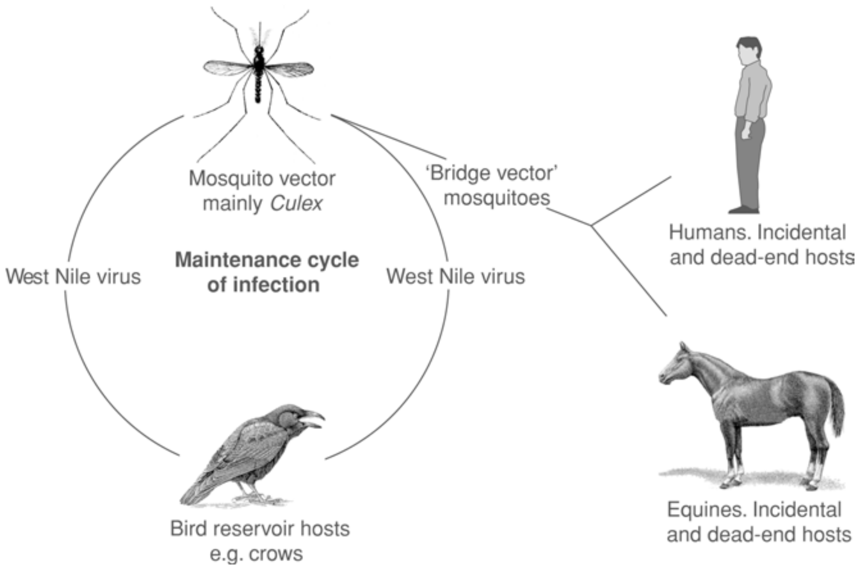


Figure 3.13 Diagrammatic representation of the transmission cycle of West Nile virus.

3.8.6 Japanese encephalitis (JE) (*Flavivirus*)

This virus is endemic in parts of China, eastern, southern and Southeast Asia and Papua New Guinea. Worldwide there are about 50 000 cases of JE annually, with 25–35% case fatality rates. Although there is a vaccine, presently mainly used in Korea, Japan, China, Thailand and Taiwan, there is a need for a cheaper, better and more widely available vaccine. The basic transmission cycle involves mosquitoes biting water birds, mainly herons, egrets and ibises, which are the principal reservoir hosts. Some infected mosquitoes bite pigs, which develop high viraemia and are termed ***amplifying hosts***. If infected mosquitoes, having bitten birds or pigs, then bite humans they transmit the virus to them. Humans, however, are dead-end hosts and consequently there is no human-to-human transmission (Fig. 3.14). Transmission to birds, humans and pigs is mainly by *Culex tritaeniorhynchus*, *Cx. vishnui* and *Cx. pseudovishnui*, all of which are ricefield-breeding mosquitoes. *Culex gelidus*, breeding in streams and ricefields, is another vector and probably maintains the virus in pig-to-pig transmissions. In southern India *Mansonia indiana* is a secondary vector.

3.8.7 Other arboviruses

There are many other mosquito-borne arboviruses infecting humans in various parts of the world, for example Ross River virus (*Alphavirus*: Australasia), Sindbis (*Alphavirus*: Africa, Asia, Australia, Europe), Murray

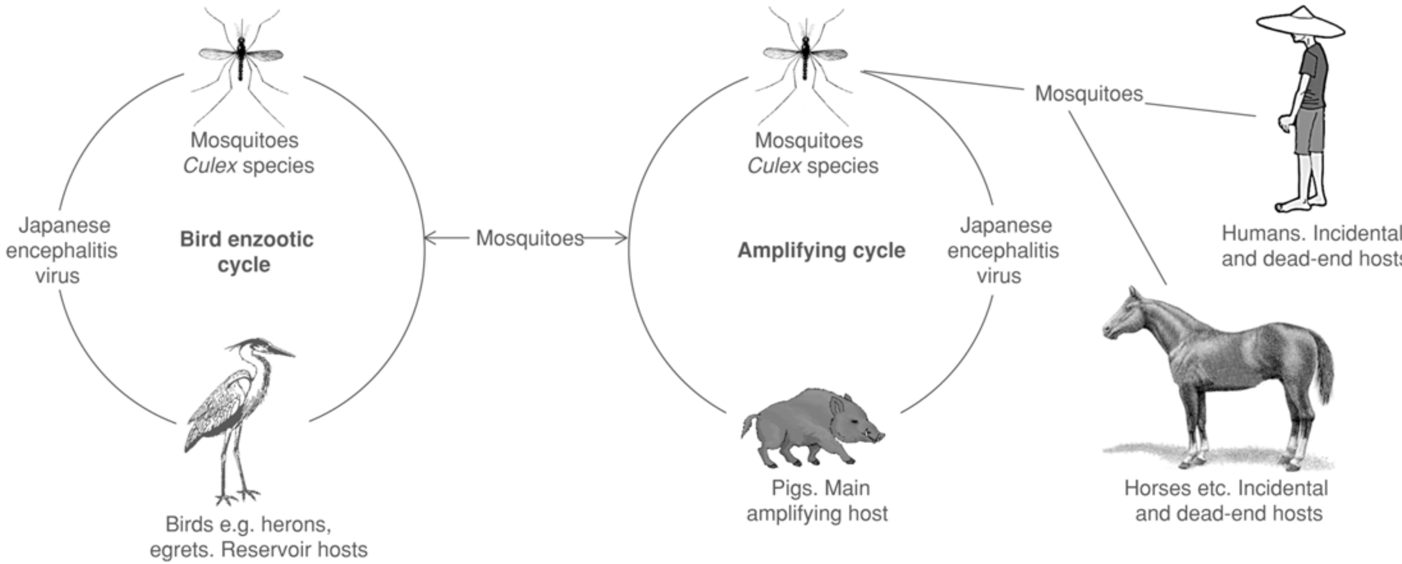


Figure 3.14 Diagrammatic representation of the transmission cycle of Japanese encephalitis virus.

Valley encephalitis (*Alphavirus*: Australia, Papua New Guinea) and Rift Valley fever (*Bunyavirus*: Africa, Saudi Arabia, Yemen). These and the more important arboviral diseases very briefly discussed below are ***zoonoses***, as of course is yellow fever.

Chikungunya (CHIK) (*Alphavirus*)

Chikungunya virus occurs in sub-Saharan Africa, the Indian subcontinent and throughout much of Southeast Asia. In 2006 large outbreaks occurred in several islands in the Indian Ocean such as Mayotte, Mauritius, Madagascar and the Seychelles and there were 244 000 cases on Réunion with more than 200 deaths. The vectors were *Ae. aegypti* and *Ae. albopictus*. As a result of these outbreaks many infected tourists returned home to North America and Europe. In 2007 there was transmission of chikungunya virus for the first time in Europe, namely in northern Italy where there were 204 confirmed cases transmitted by *Ae. albopictus*. The outbreak was contained and there was no transmission in 2008. However, the virus has since been found in Europe in 2009, 2010 and 2011.

In sub-Saharan Africa there are about five principal vectors, all *Aedes* species, such as *Ae. africanus* and *Ae. luteocephalus*, but *Ae. aegypti* is not usually an important vector, whereas in Asia it is the main vector. In 2010 in a forested area in southeastern Gabon, *Ae. albopictus* was found to be the main vector. In Africa it appears that in sylvan areas the virus can be maintained in non-human primates such as vervet monkeys (*Cercopithecus aethiops*) and baboons (*Papio ursinus*), but whether there are cases of transmission between non-human primates and humans remains speculative.

In 2010 the virus was found in non-human primates in Malaysia, but as yet the importance of this to human cases is unclear.

St Louis encephalitis (SLE) (*Flavivirus*)

In southern Canada and widely distributed in the USA, extending into Mexico, Central America, the Caribbean and South America as far south as Argentina. In eastern USA it is mainly an urban disease spread by *Cx. quinquefasciatus* or *Cx. pipiens*. ***Amplifying hosts*** are chickens and peridomestic wild birds. In western USA SLE occurs mainly in rural areas with the ricefield-breeding *Cx. tarsalis* as a vector.

Eastern equine encephalitis (EEE) (*Alphavirus*)

In Canada, but mainly in the eastern USA, and extending from Mexico through Central America as far south as Argentina, and also in the Caribbean. It is probably the most severe encephalitis virus in humans and horses. EEE is principally an infection of birds, and in North America it is spread among them mainly by *Culiseta melanura* (the genus *Culiseta* is

not discussed in this book). It is transmitted to people and horses by various species of *Aedes*, *Culex* and *Coquillettidia*.

Western equine encephalitis (WEE) (*Alphavirus*)

In Canada and the USA west of the Mississippi River, and extending into South America. This is basically an arboviral infection of birds, which are ***amplifying*** and ***maintenance*** hosts. Transmission is by *Cx. tarsalis*, a ricefield-breeding mosquito, as well as by other *Culex* and *Aedes* species. *Aedes* mosquitoes also transmit the virus to mammals, including humans and horses.

Venezuelan equine encephalitis (VEE) (*Alphavirus*)

This is a complex of six viruses found in the southern USA through Central America to the Caribbean islands and South America as far south as Argentina. The infection is often fatal in horses and other equids but usually very mild in humans. Rodents are important ***amplifying hosts*** involved in enzootic transmission cycles, while birds and bats are involved in dispersing the virus. Vectors are mainly *Culex* species. Epizootic/epidemic transmission involves equines, which are the principal amplifying hosts. *Aedes taeniorhynchus*, *Culex taeniopus* and other *Culex* species in the subgenus *Melaniconion*, as well as *Psorophora confinnis*, are important vectors.

Viraemic titres produced in humans by JE, EEE, SLE, VEE and sometimes also by WEE are so low that the infection cannot be transmitted by mosquitoes from humans to humans, or from humans to other susceptible hosts. Humans are thus ***dead-end hosts*** for these viruses, as are horses for the encephalitis viruses infecting them.

3.8.8 Filariasis

The development in mosquitoes of filarial worms causing lymphatic filariasis is briefly described in Chapter 2 in connection with the role of anopheline vectors. Both bancroftian and brugian filariasis occur in two distinct forms. The ***nocturnally periodic*** form, in which the microfilariae are in the peripheral blood only at night, is transmitted by night-biting mosquitoes such as *Anopheles*, *Mansonia* and *Culex quinquefasciatus*. During the day the microfilariae are in the blood vessels supplying the lungs, and are not available to be taken up by mosquitoes. In ***subperiodic*** forms of *Wuchereria bancrofti* and *Brugia malayi* the microfilariae exhibit a reduced periodicity and are present in the peripheral blood during the day as well as at night, but there nevertheless remains a degree of periodicity. For example, subperiodic *W. bancrofti*, such as found in Polynesia, has a small peak in microfilarial density during the daytime and can therefore be called ***diurnally subperiodic***, whereas subperiodic *B. malayi* in West Malaysia, Sumatra, Sabah, Thailand, etc. has a slight peak of microfilariae at night, and so can be called ***nocturnally subperiodic***.

There are over 100 mosquito species transmitting lymphatic filariasis, but only some of the more important species can be dealt with in the following account and in Table 3.1. For a more detailed account of the vectors see Zagaria and Savioli (2002) and Foster and Walker (2009).

Bancroftian filariasis

Wuchereria bancrofti occurs throughout much of the tropics and subtropics including South America, sub-Saharan Africa, Asia and the South Pacific. It is the most widely distributed filarial infection of humans. Bancroftian filariasis is mainly an urban disease. There are no animal reservoir hosts and the parasites develop only in mosquitoes and humans.

The ***nocturnally periodic*** form is transmitted in Asia, South America and East Africa by *Culex quinquefasciatus*. This mosquito is widespread in the tropics and its larval habitats are waters polluted with human or animal faeces or rotting vegetation and other filth; larvae are found in septic tanks, cesspits, pit latrines, drains and ditches, and in water-storage jars if they contain organically polluted water. This mosquito has increased in numbers in many towns due to increasing urbanization and the proliferation of insanitary collections of water. Adults bite at night, and after feeding they often rest in houses. Although *Cx. quinquefasciatus* is an efficient vector in much of Africa, it is a poor vector in West Africa, where most transmission of bancroftian filariasis is by *Anopheles gambiae* and *An. funestus* and the disease is principally rural. *Anopheles* species are also vectors in parts of Asia, while in Papua New Guinea *Anopheles* are the main vectors although *Culex annulirostris*, *Mansonia uniformis* and *Ae. samoana* are also important in rural areas.

In the Philippines *Aedes poicilius* is the most important vector. Adults bite in the early hours of the night, mainly indoors but also sometimes outdoors. After feeding, adults rest outdoors. Larvae occur in leaf axils of bananas, plantains and coco-yams (*Colocasia*).

The ***diurnally subperiodic*** form occurs in the Polynesian region, from where the nocturnally periodic form is absent. The most important vector is *Aedes polynesiensis*, a day-biting mosquito which feeds mostly outdoors but may enter houses to feed; adults rest almost exclusively out of doors. Larvae occur in natural containers such as split coconut shells, leaf bracts and crab-holes, and also in man-made containers such as discarded tins, pots, vehicle tyres and canoes. *Aedes pseudoscutellaris* is another outdoor day-biting mosquito that is a vector of diurnally subperiodic *W. bancrofti*, especially in Fiji. It breeds mainly in tree-holes and bamboo stumps but larvae are also found in crab-holes. *Aedes polynesiensis* is absent from New Caledonia, and here the most important vector is *Ae. vigilax*, adults of which feed outdoors mainly during the day. Larvae are found in brackish or fresh water in rock-pools and ground pools.

Table 3.1 *Summary of principal mosquito vectors of filariasis*

Species and forms of filariasis	Geographical distribution	Vectors	Zoonotic reservoir hosts
Wuchereria bancrofti			
Nocturnally periodic	Throughout tropics (except Polynesia)	*Anopheles*, *Culex quinquefasciatus*	None
	Papua New Guinea	*Aedes samoana*, *Anopheles*, *Culex annulirostris*, *Mansonia uniformis*	
	Philippines	*Aedes poicilius*, *Anopheles*	
Diurnally subperiodic	Polynesia in general	*Aedes polynesiensis*	None
	Fiji	*Aedes pseudoscutellaris*	
	New Caledonia	*Aedes vigilax*	
Nocturnally subperiodic	Thailand	*Aedes niveus*	None
Brugia malayi			
Nocturnally periodic (principally open swamps)	South Asia, from India eastwards	*Anopheles*, *Mansonia annulata*, *Ma. annulifera*, *Ma. uniformis*	Not important, possibly some exist
	China	*Aedes togoi*	
Nocturnally subperiodic (mainly in swampy forests)	Malaysia, Indonesia, Thailand, Philippines	*Mansonia bonneae*, *Ma. dives*, *Coquillettidia crassipes*	Monkeys, especially leaf-monkeys (*Presbytis* species), wild and domestic cats, pangolins
Brugia timori			
Nocturnally periodic	Alor, Timor, Flores, other Indonesian islands	*Anopheles barbirostris*	None

The ***nocturnally subperiodic*** form is found in Thailand and is transmitted by the *Aedes niveus* group of mosquitoes. Adults bite and rest outdoors; larvae are found mainly in bamboo stumps.

It should be noted that although several *Aedes* mosquitoes are vectors of filariasis, especially the bancroftian form, *Ae. aegypti* is not a vector of lymphatic filariasis. Infection rates of mosquitoes with infective larvae of *W. bancrofti* range usually from about 0.1% to 5%, depending greatly on vector species and local conditions. But in Singapore infection rates of 20% have been recorded, and in East Africa 30%.

Brugian filariasis

The ***nocturnally periodic*** form is principally a rural disease. It occurs throughout most of Asia, from southern India to Malaysia, Vietnam, Cambodia, Thailand and Indonesia. It is transmitted by night-biting mosquitoes, such as *Anopheles* species (Chapter 2) and *Mansonia* species such as *Ma. uniformis*, and in parts of India also by *Ma. annulifera*. *Mansonia* species breed in more or less permanent waters such as swamps and ponds having floating or rooted aquatic vegetation; in Kerala, India, *Ma. annulifera* also breeds in coconut soakage pits. Adults bite mainly outdoors and rest out of doors after feeding, but they may bite and rest indoors in some areas. There are no known important animal reservoirs of the nocturnally periodic form.

The ***nocturnally subperiodic*** form of *B. malayi* occurs in west Malaysia, Indonesia, Thailand and the Philippines, and is transmitted by *Mansonia* mosquitoes such as *Ma. dives*, *Ma. bonneae* and *Ma. annulifera*, and in Thailand and the Philippines also by *Coquillettidia crassipes*. Larvae of all these species occur in habitats with much vegetation, such as swampy forests. Adults bite mainly at night, although *Ma. dives* and *Ma. bonneae* may also bite during the day. This subperiodic form of *B. malayi* is a ***zoonosis*** and essentially a parasite of swamp monkeys, especially the leaf monkeys (*Presbytis* species). Humans become infected when they live at the edges of habitats harbouring these monkeys. Other reservoir hosts include *Macaca* monkeys, domestic and also wild cats, such as civets (family Viverridae) and also pangolins (i.e. scaly anteaters, genus *Manis*).

Infection rates of mosquitoes with infective larvae of *B. malayi* range from about 0.1% to 2–3%, which is slightly lower than for *W. bancrofti*, but infection rates vary according to mosquitoes and local conditions.

As mentioned in Chapter 2, the discovery of filarial worms in mosquitoes does not necessarily imply they are vectors of either *W. bancrofti* or *B. malayi*, because mosquitoes are also vectors of several other filarial parasites of animals.

3.9 Control

Repellents, mosquito nets and mosquito screening of houses and other personal protection measures (discussed in Chapters 1 and 2) can give

some relief from culicine mosquitoes. It is, however, more difficult to obtain protection from culicines than from anophelines, because many of them bite outdoors during the daytime. Spraying the interior surfaces of houses with residual insecticides, as practised for *Anopheles* control, is not usually effective for culicines, because most species do not rest in houses. Control is aimed mainly at the larvae, although aerial ultra-low-volume (ULV) insecticidal applications are sometimes used to kill adult culicine mosquitoes.

3.9.1 *Aedes* and *Psorophora*

Control of mosquitoes such as *Ae. aegypti*, *Ae. polynesiensis* and *Ae. albopictus*, species which breed mainly in man-made containers in both rural and urban areas, is often aimed at reducing the numbers of larval habitats, that is, control by ***source reduction***. Consequently people are encouraged not to store water in pots or allow water to accumulate in discarded tin cans, bottles, vehicle tyres etc. However, persuading people to cooperate in reducing peridomestic larval habitats of mosquitoes is often difficult unless local legislation is strictly enforced. A reliable piped water supply to houses can do much to reduce *Ae. aegypti* breeding.

When source reduction is not feasible, insecticides can be used on larval habitats. Suitable products include organophosphates such as fenthion, temephos and pirimphos-methyl, insect growth regulators (IGRs) such as methoprene, pyriproxyfen or diflubenzuron, or *Bacillus thurigiensis* var. *israelensis* (*Bti*). Although insecticidal spraying can kill *Aedes* and *Psorophora* larvae it usually has no effect on their eggs which have been deposited at the edges of larval habitats. However, if there are ground-based or aerial applications of granular organophosphate insecticides or IGRs these will kill the young larvae when they hatch from eggs. Such applications can be made either before or after habitats have become flooded, that is ***pre-*** or ***post-flood treatments***. Insecticidal granules landing on dry or muddy grounds remain more or less inactive until the habitats become flooded. When this occurs previously dry eggs hatch, but at the same time flooding causes the release of insecticide from the granules and this kills the newly hatched larvae. This technique helps overcome problems of controlling *Aedes* and *Psorophora* mosquitoes, whose eggs may hatch in instalments over extended periods after flooding.

Ground-based or aerial ULV application of organophosphates such as malathion, fenitrothion, pirimiphos-methyl or pyrethroids, aimed at killing adult mosquitoes, is often the most appropriate control strategy in epidemic situations.

Insecticides used to kill mosquito larvae in water intended for drinking must have extremely low mammalian toxicity; they should also impart no taste to the water. The insecticide usually recommended is temephos, in the form of 1% in briquettes or sand granules that will give a concentration of 1 mg

active ingredient per litre of water. However, some communities refuse to have their potable water dosed with any insecticide (see Chapter 1, page 28).

Yellow fever and dengue

Africa has over 90% of the world's yellow fever cases. The best defence against yellow fever is to use the attenuated 17D vaccine. Vector control, through sustained reduction of mosquito larval habitats, nevertheless still has a role in reducing the risks of yellow fever outbreaks; it also remains the main approach for dengue control, because there are presently no vaccines available for widespread use. Epidemics of dengue, and sometimes also yellow fever, can be curtailed by killing the adult vectors with aerial ULV insecticidal spraying, where the main objective is to kill infected adult mosquitoes as rapidly as possible.

To see whether *Ae. aegypti*, a vector of dengue, could be controlled by genetic modification 3.3 million sterile transgenic male *Ae. aegypti* were released in inhabited areas on the Cayman Islands in 2009. About an 80% reduction in the *Ae. aegypti* population was achieved. Then, in trials carried out in Malaysia the following year, 6000 transgenic male *Ae. aegypti* were released in uninhabited forest sites to study their dispersal and survival, after which they were killed by insecticidal spraying. Results suggested that such an approach could be used for dengue control. See *Nature* (2011) for a discussion of these trials.

3.9.2 *Culex*

Culex quinquefasciatus, an important filariasis vector, is best controlled by improving sanitation and installing modern sewage systems, but often this is not feasible and insecticides have to be used. In most areas *Cx. quinquefasciatus* is resistant to a wide range of insecticides, and this limits the choices of chemicals that can be used. Larval habitats should be sprayed every 7–10 days, and usually relatively large dosage rates are needed because most insecticides are less effective in the presence of organic pollution, which is characteristic of *Cx. quinquefasciatus* larval habitats. Chlorpyrifos and temephos are two of the more effective insecticides in polluted waters. IGRs such as methoprene, diflubenzuron and pyriproxyfen have also been used against *Cx. quinquefasciatus*.

Tipping non-toxic expanded ***polystyrene beads*** (2–3 mm) into pit latrines and cesspits to completely cover the water surface with a 2–3 cm layer suffocates larvae and pupae as well as preventing female *Cx. quinquefasciatus* from ovipositing. A single application can persist for several years and give excellent control. This is a control method that is readily accepted by most communities.

Insecticidal house-spraying, as practised against malaria vectors, and insecticide-impregnated bed-nets can be effective against *Cx. quinquefasciatus* and other *Culex* species if they are both endophilic and night-biters.

In North America ULV spraying has frequently been used against vectors of the encephalitis viruses.

Lymphatic filariasis

An estimated 1 billion people in more than 83 countries are at risk of getting lymphatic filariasis, and presently more than 120 million are infected. In 2000 the Global Programme to Eliminate Lymphatic Filariasis (GPELF) was initiated, with the aim of achieving this goal by 2020. China had one of the highest incidences of lymphatic filariasis, but by 2008 China, and also Korea and Egypt, had eliminated lymphatic filariasis as a public health problem.

Control strategies involve mass distribution of microfilarial drugs administered annually, using albendazole and ivermectin in sub-Saharan Africa, and elsewhere albendazole plus diethylcarbamazine. In addition, vector populations can be reduced by using suitable chemical larvicides and the microbial agents *Bacillus thuringiensis* var. *israelensis* (*Bti*) and *B. sphaericus*, tipping expanded polystyrene beads into pit latrines and septic tanks to prevent mosquito breeding, use of insecticide-impregnated bed-nets, and possibly residual house-spraying. All of these should reduce densities of *Cx. quinquefasciatus*, a very important filariasis vector. In contrast, it is very difficult to reduce populations of *Mansonia* mosquitoes, important filariasis vectors in Asia, because adults rarely rest or bite indoors and larval habitats are often large and relatively inaccessible: see below.

3.9.3 *Mansonia*

Mansonia mosquitoes are usually controlled either by removing aquatic weeds upon which the larvae and pupae depend for their oxygen requirements, or by using herbicides to kill the weeds. Removing weeds, however, may result in ecological changes that allow aquatic habitats to become colonized by mosquito species that were previously excluded by the dense covering of weeds.

Insecticidal granules or pellets are more suitable than liquid formulations for killing *Mansonia* larvae, because they penetrate vegetation, sink to the bottom of larval habitats and release their insecticidal contents through the water. However, species such as *Ma. dives* and *Ma. bonneae*, which are important vectors of brugian filariasis, breed in extensive swampy inaccessible forests where control is impractical.

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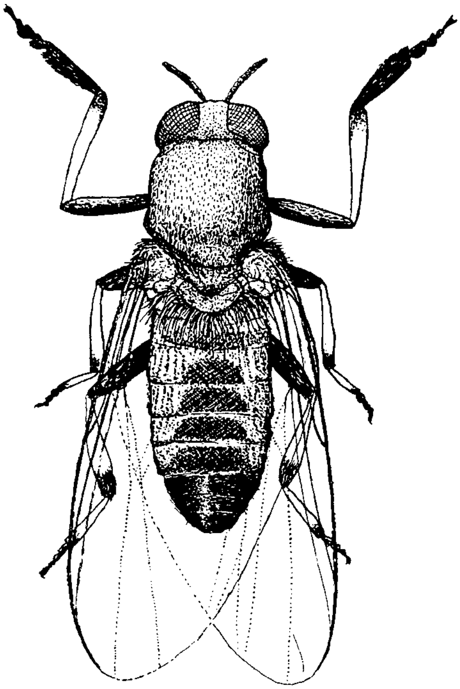
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See also references at the ends of Chapters 1 and 2.

4

Black flies (Simuliidae)



Black flies belong to the family Simuliidae and have a worldwide distribution. There are more than 2000 species in 25 genera. However, only three genera, *Simulium*, *Prosimulium* and *Austrosimulium*, contain species that commonly bite people.

Medically, *Simulium* is by far the most important genus as it contains many vectors. In Africa, species in the *S. damnosum* complex and the *S. neavei* group, and in Central and South America, species in the *S. ochraceum*, *S. metallicum* and *S. exiguum* complexes, transmit the parasitic nematode *Onchocerca volvulus*, which causes human onchocerciasis (river blindness). In Brazil, *S. amazonicum* transmits *Mansonella ozzardi*, a filarial parasite that is usually regarded as non-pathogenic.

The Simuliidae are commonly known as black flies, but in some areas, especially Australia, they may be called sand flies. As explained in Chapter 5, this latter terminology is confusing and best avoided because biting flies in the family Ceratopogonidae are sometimes also called sand flies, while flies in the subfamily Phlebotominae are regarded as the true sand flies.

4.1 External morphology

Adult black flies are quite small, about 1.5–4 mm long, relatively stout-bodied and, when viewed from the side, have a rather ***humped*** thorax. As their vernacular name indicates they are usually ***black*** in colour (Plate 5), but some species have contrasting patterns of white, silvery or yellowish hairs on their bodies and legs, while others may be predominantly orange or bright yellow.

Black flies have a pair of large compound eyes, which in females are separated on the top of the head (a condition known as ***dichoptic***) whereas in males the two eyes touch each other and occupy most of the head (a condition known as ***holoptic***). In males, but not females, the lenses of the eyes are larger on the upper half than on the lower half (Fig. 4.1b). The antennae are short, stout, cylindrical and distinctly segmented (usually 11

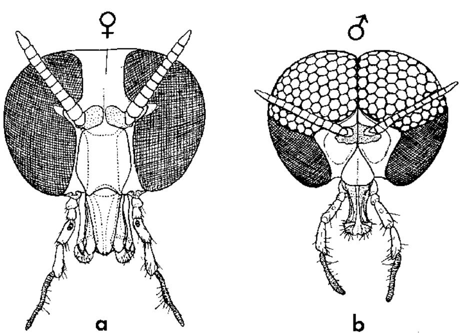


Figure 4.1 Front view of adult *Simulium* heads: (a) female with dichoptic eyes; (b) male with holoptic eyes.

segments) and lack long hairs. The mouthparts are short and relatively inconspicuous, but the five-segmented maxillary palps hang downwards and are easily seen. ***Only females*** bite. The mouthparts, being short and broad, do not penetrate deeply into the host's tissues. Teeth on the labrum stretch the skin, while the rasp-like action of the maxillae and mandibles cuts through the skin and ruptures its fine blood capillaries. The small pool of blood produced is then sucked up by the fly. This method of feeding is ideally suited for picking up the microfilariae of *Onchocerciasis volvulus*, which occur in human skin, not blood. Morphologically the mouthparts are similar to those of the biting midges (Ceratopogonidae, Chapter 6).

The thorax is covered dorsally with very fine and appressed hairs, which can be black, white, silvery, yellow or orange and may be arranged in various patterns. The relatively short legs are also covered with very fine and closely appressed hairs and may be unicolourous or have contrasting pale and dark bands. Each tarsus has a pair of claws, which are untoothed (i.e. simple) in mammal-feeders.

Wings are characteristically short and broad and ***lack*** both scales and prominent hairs. Only the veins near the anterior margin are well developed; the rest of the wing is membranous and has indistinct venation (Fig. 4.2, Plate 5). The wings are colourless or almost so, and when at rest are closed over the body like the blades of a closed pair of scissors.

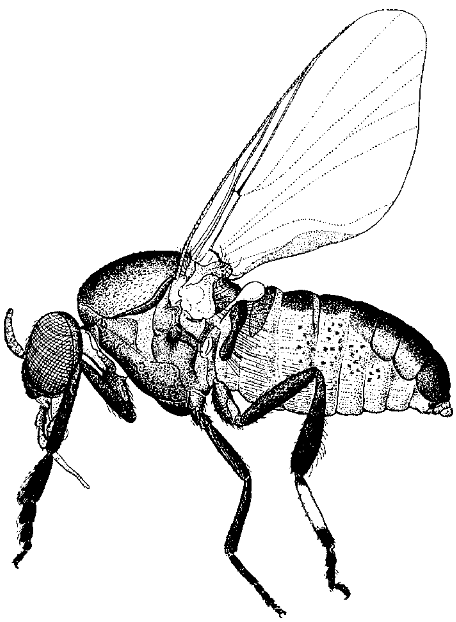


Figure 4.2 Adult simuliid black fly (*Simulium damnosum*) in lateral view. (Courtesy of R. W. Crosskey and the Natural History Museum, London.)

The abdomen is short and squat, and covered with inconspicuous closely appressed fine hairs. In neither sex are the genitalia very conspicuous. Black flies are easily ***sexed*** by looking to see whether their eyes are dichoptic (females) or holoptic (males).

4.2 Life cycle

Eggs are about 0.1–0.4 mm long, brown or black, and are more or less triangular in shape but have rounded corners and smooth unsculptured shells (Fig. 4.3a) and are covered with a sticky substance. Eggs are always laid in ***flowing water***, but the type of larval habitat differs greatly according to species. Habitats can vary from small trickles of water, slow-flowing streams, lake outlets and water flowing from dams to fast-flowing rivers and rapids. Some species prefer lowland streams and rivers whereas others are found in mountain rivers. In species such as *S. ochraceum*, a Central American vector of onchocerciasis, eggs are scattered over the surface of flowing water while females are in flight. In most species, however, ovipositing females alight on partially immersed objects such as rocks, stones and vegetation to lay some 150–800 eggs in sticky masses or strings. Females

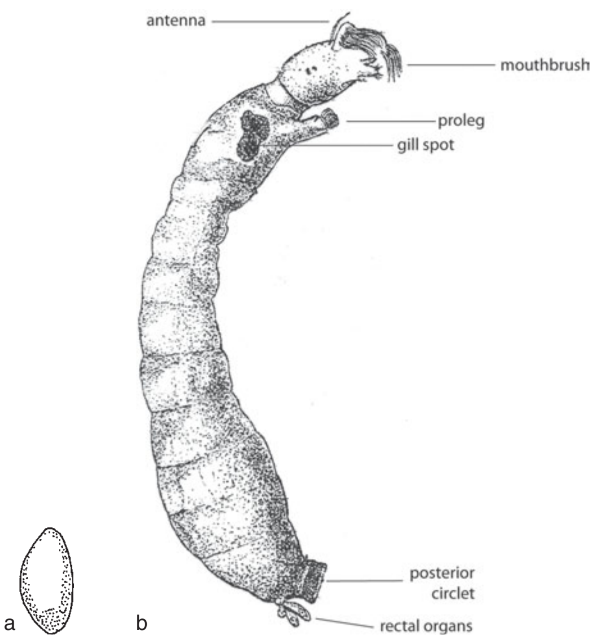


Figure 4.3 (a) *Simulium* egg; (b) lateral view of the last larval instar, showing principal diagnostic simuliid characters. The species figured is *Simulium damnosum*, a species which has the body covered with minute dark setae and has small dorsal tubercles, i.e. small humps.

may crawl underneath the water and become completely submerged during oviposition. There are sometimes a few favoured oviposition sites in a stream or river, resulting in thousands of eggs from many females being found together. *Simulium damnosum*, for example, frequently has such communal oviposition sites. Eggs are unable to survive desiccation.

Eggs of *S. damnosum* hatch within about 1–2 days, but in many other tropical species the egg stage lasts 2–4 days. Eggs of species inhabiting temperate or cold northern areas may not hatch for many weeks, and some species pass the winter as diapausing eggs.

There are six to eleven (usually seven) larval instars and a mature larva, depending on the species, is about 4–12 mm long. It is easily distinguished from all other aquatic larvae (Fig. 4.3b). The head is black, or almost so, and has a prominent pair of ***feeding brushes*** (cephalic fans), while the weakly segmented cylindrical body is usually greyish, but may be darker or sometimes even greenish. The body is slightly swollen beyond the head and in most, but not all, species distinctly swollen towards its end. Ventrally, just below the head, is a small thoracic ***proleg*** which is armed with a small circlet of hooklets. The rectum has a finger-like rectal organ which on larval preservation may be extruded and visible as a dorsal protuberance towards the end of the abdomen.

Larvae do not swim but remain sedentary for long periods on submerged vegetation, rocks, stones and other debris. Attachment is achieved by the ***posterior hook-circlet*** (anal sucker of many previous authors) tightly gripping a small silken pad which has been produced by the larva's very large salivary glands and which is firmly glued to the substrate. Larvae can nevertheless move about. This is achieved by alternately attaching themselves to the substrate by the proleg and the posterior hook-circlet, which results in their moving in a looping manner. When larvae are disturbed they can deposit sticky saliva on a submerged object, release their hold and be swept downstream for some distance at the end of a silken thread. They can then either swallow the thread of saliva and regain their original position, or re-attach themselves at a site further downstream.

Larvae normally orientate themselves to lie ***parallel*** to the flow of water with their heads downstream. They are mainly filter-feeders, ingesting, with the aid of large feeding brushes, suspended particles of food. However, a few species have predaceous larvae and others are occasionally cannibalistic. Depending on species and temperature, larval development may be as short as 6–12 days, but in some species it may be extended to several months, and in other species larvae overwinter.

Mature larvae can be recognized by a blackish mark termed a ***gill spot*** (respiratory organ of the future pupa) on each side of the thorax (Fig. 4.3b). These larvae spin, with the silk produced by their salivary glands, a protective slipper-shaped brownish ***cocoon***. This is firmly attached to submerged vegetation, rocks or other objects, and its shape and structure

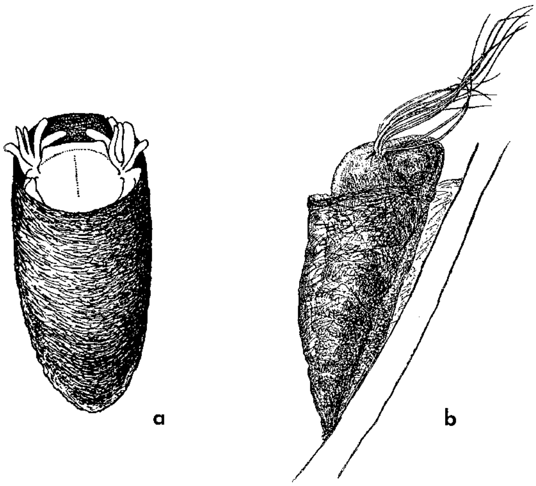


Figure 4.4 *Simulium* pupae in their cocoons: (a) dorsal view of a species (*S. damnosum*) with broad and short respiratory filaments (courtesy of R. W. Crosskey and the Natural History Museum, London); (b) lateral view of a species (*S. striatum*) with long and thin respiratory filaments.

vary greatly according to species (Fig. 4.4). After weaving the cocoon the enclosed larva pupates. The pupa has a pair of thin-walled ***respiratory gills***, which are usually prominent and may be filamentous or broad. Their length, shape and number of filaments or branches provide useful taxonomic characters for species identification. These gills, and the anterior part of the pupa, often project from the entrance of the cocoon (Fig. 4.4). In both tropical and non-tropical countries the pupal period lasts only 2–6 days and is unusual in not appearing to be dependent on temperature. On emergence adults either rise rapidly to the water surface in a protective bubble of gas, which prevents them from being wetted, or they escape by crawling up partially submerged objects such as vegetation or rocks. A characteristic of many species is the almost simultaneous mass emergence of thousands of adults. On reaching the water surface the adults immediately take flight.

The empty pupal cases, with gill filaments still attached, remain enclosed in their cocoons after the adults have emerged and provide a means of identifying simuliid species that have successfully emerged.

A few African and Asian black fly species have a very unusual aquatic association. For example, in East Africa larvae and pupae of *S. neavei* do not occur on submerged rocks or vegetation but on other aquatic arthropods, such as the immature stages (nymphs) of mayflies (Ephemeroptera), and various crustaceans including freshwater crabs. Such an association is termed a ***phoretic*** relationship. As eggs are not found on these animals they are probably laid on submerged stones or vegetation.

Nuclei of the larval salivary gland cells have large ***polytene chromosomes*** which have banding patterns that are used to identify otherwise morphologically identical species within a species complex. For example, chromosomal studies have shown that there are 57 cytoforms in the *S. damnosum* complex, many of which are known to be distinct species and have scientific names.

4.2.1 Adult behaviour

Both male and female black flies feed on plant juices and naturally occurring sugary substances, but ***only females*** take blood-meals. Biting occurs out of doors during the day. Many species, including *S. damnosum* in Africa, have bimodal biting patterns, with peak biting in the early morning and again in the afternoon or early evening. However, in some species, such as *S. ochraceum* in Guatemala, biting continues more or less throughout the day. Many species seem particularly active on cloudy, overcast days and in thundery weather. Black flies may exhibit marked preferences for feeding on different parts of the body; for example, *S. damnosum* feeds mainly on the legs whereas *S. ochraceum* prefers to bite the head and torso. When feeding on animals, adults crawl down the fur of mammals, or feathers of birds, to bite the host's exposed skin; they may also enter the ears to feed.

Many species of black fly feed almost exclusively on birds (***ornithophagic***), others on non-human mammalian hosts (***zoophagic***), while several species also bite people (***anthropophagic***). Some of these, however, prefer various large animals such as donkeys or cattle and bite humans only as a second choice, whereas other species find humans almost equally attractive hosts; no species feeds exclusively on people. After feeding, blood-engorged females shelter in vegetation, on trees and in other natural outdoor resting places until the blood-meal is completely digested. In the tropics this takes 2–3 days, while in non-tropical areas it may take 3–8 days or longer, the speed of digestion depending mainly on temperature. A few species can lay eggs without a blood-meal (i.e. they are ***autogenous***). Relatively little is known about black fly longevity, but it seems that adults of most species live for 3–4 weeks.

Females of some species may fly considerable ***distances*** (15–30 km) from their emergence sites to obtain blood-meals. They may also be dispersed long distances by winds. For example, it is not exceptional for adults of *S. damnosum* to be found biting 60–100 km from their larval habitats, and in West Africa there is evidence that prevailing winds can carry adults up to 400–600 km. These long distances can hinder control programmes, because areas freed from black flies can be reinvaded from distant larval habitats. In Central and South America black flies generally disperse only about 2–15 km.

In Europe and temperate and northern areas of America and Asia (i.e. the Palaearctic region) the biting nuisance from simuliids is seasonal. This is because adults die in the autumn and new generations do not appear until the following spring or early summer. In many tropical areas there is continuous breeding throughout the year, but there may nevertheless be dramatic increases in population size during the rainy season.

4.3 Medical importance

4.3.1 Annoyance

In both tropical and non-tropical regions black flies can cause very serious biting problems. Although the severity of the reaction to bites differs in different individuals, localized swelling and inflammation frequently occurs, often accompanied by intense irritation lasting for several days, or even weeks. Repeated biting by black flies such as *S. erythrocephalum* in central Europe, *S. posticatum* in England, *S. venustum* and *S. vittatum* in North America can cause headaches, fevers, swollen lymph glands and aching joints. In some areas of North America outdoor activities are almost impossible at certain times of the year due to the intolerable numbers of biting simuliids. The classical example of the nuisance caused by black flies was the seasonal exodus during the eighteenth century of people from the Danube valley area in central Europe, largely to save their livestock from attack by enormous numbers of *S. colombaschense*. However, it is as disease vectors that black flies are most important medically.

4.3.2 Onchocerciasis

Onchocerciasis is a non-fatal disease, often called river blindness, that is caused by the filarial parasite *Onchocerca volvulus*. There are no animal reservoir hosts, so the disease is not a zoonosis. Worldwide an estimated 37 million people are infected, of whom about 300 000 are blind or partially blind in 37 countries where the disease is endemic. About 99% of all cases occur in 30 countries in West Africa, Central Africa and much of East Africa. Yemen also has a few cases of onchocerciasis. In the Americas 500 000 people are at risk of getting onchocerciasis, and 180 000 are infected in localized areas of Brazil, Colombia, Ecuador, Guatemala, Mexico and Venezuela.

Black flies are the only vectors of human onchocerciasis. Their habit during feeding of tearing and rasping the skin to rupture blood capillaries makes them particularly suited to the ingestion of the ***skin-borne microfilariae*** of *O. volvulus*. Most microfilariae ingested during feeding are destroyed or excreted, but some penetrate the stomach wall and migrate to the thoracic muscles. Here they develop into sausage-shaped stages (called L_1 larvae), then moult to L_2 stage larvae, a few of which moult

again to become elongate and thinner L_3 worms which pass through the head and down the proboscis. These ***infective third-stage*** worms (about 660 μm in length) leave the proboscis and penetrate the host's skin when black flies feed. The interval between the ingestion of microfilariae and the time when infective larvae (L_3) are in the proboscis is about 6–12 days, depending on temperature.

African vectors of onchocerciasis

Chromosomal studies show that the *S. damnosum* complex is composed of about 57 cytoforms, many of which merit species status. The *S. damnosum* species complex is widespread in tropical Africa, and some of the species are the most important vectors of onchocerciasis.

Adults of the *S. damnosum* species complex are mainly black. They can be recognized by their broad and flattened front tarsi having a conspicuous dorsal crest of fine hairs, and by a very broad white area on the first segment of the hind tarsus (basitarsus) (Fig. 4.2). Larvae are more or less covered with fine setae, and there are usually prominent dorsal abdominal tubercles (Fig. 4.3b). Branches of the pupal respiratory gills are thick and finger-like and are located within the neck of the cocoon (Fig. 4.4a). The immature stages are found in the rapids of small or very large rivers in both savanna and forested areas of Africa. Adults frequently disperse hundreds of kilometres from their larval habitats. The vectorial status of species within the *S. damnosum* complex varies, the most important vectors of onchocerciasis being *S. damnosum* s. str., *S. sirbanum*, *S. sanctipauli* and *S. leonense*.

Other, but much less important, vectors include *S. neavei*, which is responsible for transmission in the Democratic Republic of the Congo and Uganda. *Simulium neavei* is a ***phoretic*** species. That is, the larvae and pupae are attached to other freshwater fauna, mainly crabs of the genus *Potamonautes* and mayfly (Ephemeroptera) nymphs, both of which occur in small, rocky, rather turbid streams and rivers. *Simulium neavei* was eradicated from Kenya in the 1950s by bush clearing and insecticidal dosing of streams.

American vectors of onchocerciasis

Only eight species are involved in transmission in the Americas, and only the more important ones are mentioned here. *Simulium ochraceum* is widely distributed in Central America and northern parts of South America and is the principal onchocerciasis vector in southern Mexico and Guatemala. Adults are very small and are easily recognized by their dark brown legs, bright orange scutum (dorsal surface of the thorax) and yellow basal part of the abdomen, which contrasts with the black apical part. Females oviposit while in flight, dropping their eggs onto floating vegetation. Larval habitats

consist of trickles of flowing water and very small streams, often concealed by bushes, vegetation and fallen leaves. Adults do not appear to disperse far. The main biting season is unusual in being in the drier months of the year.

Simulium metallicum occurs in Mexico and through Central America to northern areas of South America. In northern Venezuela it appears to be the most important vector, whereas in other areas such as in Mexico and Guatemala it is considered a minor vector. It is a black species and has a broad white area on the first segment of the hind tarsus. Larvae occur in small or large streams and rivers. Adults fly further from their larval habitats than do those of *S. ochraceum*.

Simulium exiguum is the only known vector in Colombia, and a primary vector in Ecuador. Above 150 m in the Brazilian Amazonas the main vector is *S. guianense*; below this height the vector is *S. oyapockense*.

4.3.3 *Mansonella ozzardi*

Mansonella ozzardi is a filarial parasite of humans that is usually regarded as non-pathogenic, although it has been reported as causing morbidity in Colombia and Brazil. It is transmitted in the Caribbean islands, Trinidad, Surinam and also Argentina by *Culicoides* species, mainly *C. furens* and *C. phlebotomus* (Chapter 6), but in northwestern Argentina, Brazil, Colombia, Guyana, Venezuela and southern Panama *S. amazonicum* is the main vector.

4.4 Control

Some protection can be gained by using repellents such as DEET, or by wearing pyrethroid-impregnated or sprayed clothing.

However, the only practical control method is to apply insecticides to larval habitats. These need be applied to only a few selected sites on watercourses for some 15–30 minutes, because as the insecticide is carried downstream it kills simuliid larvae over long stretches of water. Flow rates of the water and its depth are used to calculate the quantity of insecticide to be released. In the past dosing rivers with DDT has given good control of *S. damnosum* in Africa, but because of its accumulation in food chains DDT is no longer used. Nowadays insecticides such as temephos or *Bacillus thuringiensis* var. *israelensis* (*Bti*) are often used. Treatment has to be regularly repeated, sometimes at intervals of 1–2 weeks, throughout the year to prevent recolonization. In Guatemala insecticide-treated briquettes have been used to control *S. ochraceum*, which breeds in small rivers.

In many areas ground application of larvicides is difficult, either because of the enormous size of the rivers requiring treatment or because breeding

occurs in a large network of inaccessible small streams and watercourses. Under these conditions aerial applications from small aircraft or helicopters may be appropriate.

4.4.1 Onchocerciasis control programmes

Because of the severity of river blindness in the Volta River Basin area of West Africa and its devastating effect on rural life, the world's most ambitious and largest vector control programme, the Onchocerciasis Control Programme (OCP), was initiated in 1974 by the World Health Organization (WHO). The programme was operational between 1974 and 2002. By 1986 there were 11 participating countries, namely Benin, Burkina Faso, Ivory Coast, Ghana, Mali, Niger and Togo all receiving vector control, and Bissau, Guinea Bissau, Senegal and Sierra Leone without vector control but receiving community treatment with ivermectin. In countries having vector control, rivers over an area of 1.3 million km^2 that were breeding the *S. damnosum* species complex were dosed weekly with aerial applications of temephos. Because of the appearance of temephos resistance in 1980 in some populations and species of the *S. damnosum* species complex, some rivers were treated with other insecticides or with *Bacillus thuringiensis* var. *israelensis* (*Bti*). In 1982, to hinder the spread of further resistance, different insecticides such as the organophosphates phoxin, pyraclofos and temephos and the pyrethroids permethrin and etofenprox were used in rotation.

In 1988 the OCP started large-scale distribution of the microfilaricidal drug ***ivermectin*** (Mectizan), which was given orally to people once or twice a year. In many areas vector control was included in this strategy. The programme was very successful, and by 2008 onchocerciasis was no longer a public health problem, except in Sierra Leone and some areas of Benin, Guinea and Togo.

In 1995 the African Programme for Onchocerciasis Control (APOC) was created to cover populations at risk in 19 countries outside the OCP. The objective was to establish, within 12 years, a sustainable community-based ivermectin treatment regimen, backed up with focal larviciding in some areas. Because ivermectin does not kill adult worms, control needs to continue for about 20–25 years to allow time for the reservoir of infection (adult onchocercal worms) in the human population to die out. Since APOC was launched 40 million people have been treated annually with ivermectin. The long-term objective is to eliminate blindness caused by onchocerciasis by 2020.

An estimated 95% of the population in Central and South America at risk of onchocerciasis live in Mexico, Guatemala and Venezuela. There are 13 main endemic areas in the Americas. In 1993 the Onchocerciasis Elimination Programme for the Americas (OEPA) was launched, which

was based mainly on the distribution of ivermectin every six months. It was estimated that if 85% or more of the infected people were treated the disease could be eradicated. In 2007 Colombia became the first country in the world to have halted transmission of river blindness, and a further six of the endemic foci, and one subfocus of transmission, have probably also interrupted transmission. The hope was to stop transmission by 2007, but this was later changed to stopping transmissiom by 2012.

In 2007 resistance to ivermectin in *O. volvulus* was reported from Ghana. This has stimulated greater efforts to find new drugs, one of which is Moxidectin, which appears will be more effective than ivermectin.

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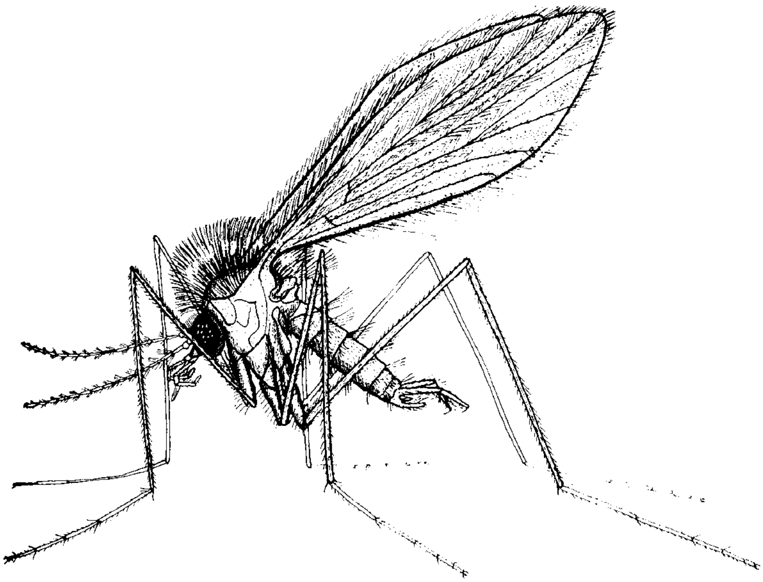
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5

Phlebotomine sand flies (Phlebotominae)



Within the subfamily Phlebotominae of the family Psychodidae it is estimated that there are approaching 1000 species and subspecies of sand flies, in five or six genera (depending on whether *Psychodopygus* is considered a subgenus or genus). Three genera – *Phlebotomus*, *Lutzomyia* and *Sergentomyia* – suck blood from vertebrates, the former two being the more important because they contain disease vectors.

The genus *Phlebotomus* occurs only in the Old World, from southern parts of northern temperate areas, mainly the Mediterranean region, to central Asia, and in tropical areas, but there are not many species in sub-Saharan Africa or Southeast Asia and none in the Pacific area. Most *Phlebotomus* species inhabit semiarid and savanna areas in preference to forests. *Lutzomyia* species are found only in the New World, and, by contrast, occur mainly in forested areas of Central and South America.

Sergentomyia species are also confined to the Old World, being found mainly in the Indian subregion, sub-Saharan Africa and Asia. Although a few species bite people they are not vectors.

The medically most important species include *Phlebotomus papatasi*, *P. sergenti*, *P. argentipes*, *P. ariasi*, *P. perniciosus* and species in the *Lutzomyia longipalpis* and *L. flaviscutellata* species complexes. In both the Old and New Worlds sand flies are vectors of leishmaniasis and viruses responsible for sand fly fever, and in the Andes the bacterium *Bartonella bacilliformis*, causing bartonellosis (Carrión's disease).

Adult flies are often called sand flies because of their colour. However, this can be confusing, because in some parts of the world the small biting midges of the family Ceratopogonidae (Chapter 6) and black flies (Simuliidae, Chapter 4) are called sand flies.

5.1 External morphology

Adults of *Phlebotomus* and *Lutzomyia* are difficult to distinguish, but as the former genus is found only in the Old World and the latter in the New World this is not a problem.

Adult phlebotomine sand flies are readily recognized by their minute size (usually less than 5 mm long), hairy appearance, relatively large black eyes and long and ***stilt-like*** legs (Plate 6). The only other blood-sucking flies which are as small as this are some species of biting midges (Ceratopogonidae), but these have non-hairy wings and differ in many other details (Chapter 6). Phlebotomine sand flies have the head, thorax, wings and abdomen densely covered with long hairs. The 16-segmented ***antennae*** are long and composed of small bead-like segments having short hairs; antennae are similar in both sexes. The mouthparts are short and inconspicuous and adapted for blood-sucking, but ***only females*** bite. At their base is a pair of five-segmented maxillary palps which are relatively conspicuous and droop downwards.

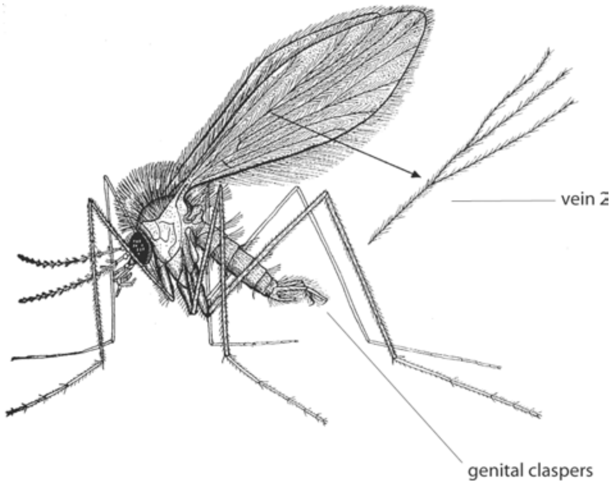


Figure 5.1 Adult male phlebotomine sand fly, showing genital claspers at end of abdomen, and a diagrammatic representation of the double branching of wing vein 2.

Wings are lanceolate in outline and quite distinct from the wings of other biting flies. The Phlebotominae can be distinguished from other subfamilies of the family Psychodidae, which they may superficially resemble, by their ***wings***. In sand flies the wings are held at an angle of about 40 degrees over the body when the fly is at rest or blood-feeding, whereas in non-biting psychodid flies they are folded roof-like over the body or held flat across the body. Wing venation also differs. In phlebotomine sand flies, but not in the other subfamilies of Psychodidae, ***vein 2 branches twice***, although this may not be apparent unless most of the hairs are rubbed from the wing veins (Fig. 5.1).

The abdomen is moderately long and in the female more or less rounded at the tip. In males it terminates in a prominent pair of genital claspers (Fig. 5.1) which give the end of the abdomen an upturned appearance.

Identification of adult phlebotomine sand flies to species is difficult and usually necessitates the examination of internal structures, such as the arrangement of the teeth on the cibarial armature, the shape of the spermatheca in females, and in males the structure of the external genitalia (terminalia).

5.2 Life cycle

The minute eggs (0.3–0.4 mm) are more or less ovoid in shape and usually brown or black, and careful examination under a microscope reveals that they are patterned, as shown in Figure 5.2. Some 30–70 eggs are laid singly at each oviposition. They are thought to be deposited in small cracks and holes in the ground, at the base of termite mounds, in cracks in masonry, on stable floors, in poultry houses, amongst leaf litter and in the Americas

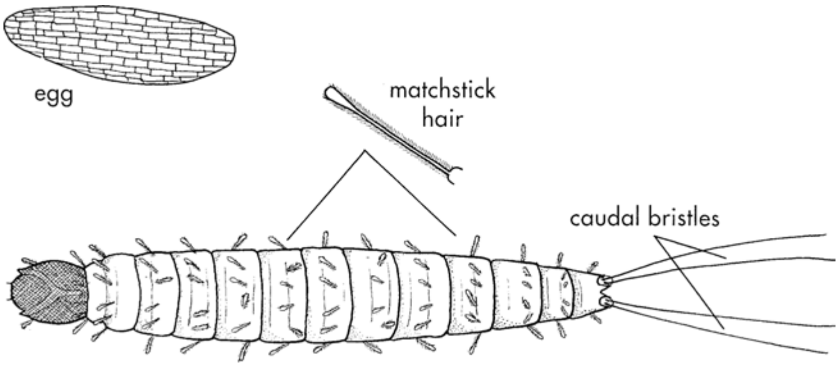


Figure 5.2 Egg of a phlebotomine sand fly, showing mosaic-type pattern, and a 12-segmented larva with matchstick hairs and caudal setae.

between buttress-roots of forest trees. The type of oviposition site presumably varies greatly according to species.

Although eggs are not laid in water they require a microhabitat with high humidity. They are unable to withstand desiccation and hatch after 4–20 days, although hatching may likely be delayed in cooler weather. Larvae are mainly scavengers, feeding on organic matter such as fungi, decaying forest leaves, semi-rotting vegetation, animal faeces and decomposing bodies of arthropods. Although some species, especially of the genus *Phlebotomus*, occur in semiarid areas, the actual larval habitats must have a high degree of humidity. Larvae may be able to survive by migrating to drier areas if their breeding places are temporarily flooded.

There are four larval instars. The mature larva is 3–6 mm long and has a well-defined black head which is provided with a pair of small mandibles; the body is white or greyish and has 12 segments (Fig. 5.2). Ventrally the abdominal segments have small pseudopods, but the most striking feature is the presence on the head and all body segments of conspicuous thick bristles with feathered stems, which in many species have slightly enlarged tips. They are called ***matchstick*** hairs, and they identify larvae as those of phlebotomine sand flies. In most species the last abdominal segment bears two pairs of conspicuous long hairs called the ***caudal setae***. First-instar larvae have two single bristles, not two pairs.

Larval development is usually completed after 20–30 days, the duration depending on the species, temperature and availability of food. In temperate areas and arid regions sand flies may overwinter as diapausing fully grown larvae. Prior to pupation the larva assumes an almost erect position in the habitat, the skin then splits open and the pupa wriggles out. The larval skin is not completely cast off but remains attached to the end of the pupa. The presence of this skin, with its characteristic two pairs of caudal bristles, aids in the recognition of the phlebotomine pupa. The pupal shape is as shown in Figure 5.3. Adults emerge from the pupae after about 6–13

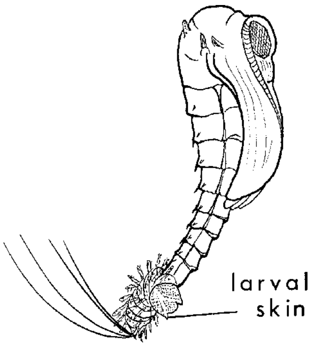


Figure 5.3 Pupa of a phlebotomine sand fly, with larval skin still attached.

days. The life cycle, from oviposition to adult emergence, is 30–60 days, but extends to several months in some species with diapausing larvae. In temperate areas adults die off in late summer or autumn and species overwinter as larvae, with the adults emerging the following spring. It is usually extremely difficult to find larvae or pupae of sand flies, and relatively little is known about their biology and ecology.

5.2.1 Adult behaviour

Both sexes feed on plant juices and sugary secretions, but ***females*** in addition suck blood from a variety of vertebrates, including livestock, dogs, urban and wild rodents, snakes, lizards and amphibians; a few species feed on birds. Females of many *Phlebotomus* species in the Old World and *Lutzomyia* species in the New World bite mammals, including humans. Biting is usually restricted to crepuscular and nocturnal periods, but people may be bitten during the day in darkened rooms, or in forests during overcast days. Most species feed out of doors (***exophagic***) but some species also feed indoors (***endophagic***). A few species are ***autogenous***, that is they can lay eggs without blood-feeding.

Adults are ***weak fliers*** and usually disperse 100 m or less from their larval habitats. Consequently biting is often very localized. However, adults of at least some species have been known to fly up to 2.2 km over a few days. When close to a host sand flies may have a characteristic hopping type of flight, so that there may be several short flights and landings before females settle on a host. Even a light wind inhibits flight activities and biting. Because of their very short mouthparts sand flies are unable to bite through clothing.

During the day adult sand flies rest in sheltered, dark and humid sites, but on dry surfaces, such as on tree trunks, on ground litter and foliage of forests, in animal burrows, termite mounds, tree-holes, rock fissures, caves, cracks in the ground and inside human and animal habitations. Species that commonly rest in houses (***endophilic***) before or after feeding on humans

are often referred to as domestic or peridomestic species. Examples are *Phlebotomus papatasi* in the Mediterranean area, *P. argentipes* in India and the *Lutzomyia longipalpis* species complex in South America.

In temperate areas of the Old World sand flies are seasonal and adults occur only in the summer months. In tropical areas some species are common more or less throughout the year, but in other species there may be well-marked changes in abundance of adults related to the dry and wet seasons.

5.3 Medical importance

5.3.1 Annoyance

About 70 species are vectors of disease to humans, but apart from their importance as vectors, sand flies may constitute a serious, but usually localized, biting nuisance. In the Americas up to 100 bites per night have been recorded. In previously sensitized people their bites may result in severe and almost intolerable irritations, a condition known in the Middle East as harara.

5.3.2 Leishmaniasis

Leishmaniasis is a term used to describe a number of closely related diseases caused by about 30 distinct species, subspecies and strains of *Leishmania* parasites. Worldwide there are about 1–2 million cases a year, with about 12 million people currently infected in 88 countries. The three main clinical forms are cutaneous, mucocutaneous and visceral leishmaniasis. A fourth, less common form is diffuse cutaneous leishmaniasis, while post-kala-azar dermal leishmaniasis is caused by *Leishmania donovani donovani* following cure of the initial visceral form. The epidemiology of leishmaniasis is complex, involving not only different parasite species but different strains of parasites and different reservoir hosts.

Basically ***amastigote*** parasites ingested by female sand flies with a blood-meal multiply in the gut and develop into ***promastigotes***, which are elongate, have a flagellum and attach to the mid-gut or hind-gut wall and multiply rapidly. Many, however, are voided when the fly defecates. After further development the survivors migrate to the anterior part of the mid-gut and then to the fore-gut. Here some parasites become ***metacyclic*** forms. Four to 25 days after the sand fly has taken an infective blood-meal the metacyclic forms are found in the mouthparts, and are introduced into a new host during feeding. Infective flies frequently probe more often than uninfected flies, thus maximizing transmission of parasites during blood-feeding. Previous feeding by females on sugary substances, mostly obtained from plants, is essential not only for the survival of the sand fly but also for the development of the parasites to the infective form.

Most types of leishmaniasis are ***zoonoses***. The degree of involvement of humans varies greatly from area to area. The epidemiology is largely

determined by the species of sand flies, their ecology and behaviour, the availability of a wide range of non-human hosts, and also by the species and strains of *Leishmania* parasites. In some areas, for example, sand flies will transmit infections almost entirely among wild or domesticated animals, with little or no human involvement, whereas elsewhere animals may be important ***reservoir hosts*** of infection for humans. In India infections may be transmitted between people by sand flies, with animals taking no identifiable part in transmission. The epidemiology of the leishmaniases is complex, and only simplified accounts are given below.

Cutaneous leishmaniasis (CL)

In the Old World, CL is known also as ***oriental sore***. It occurs mainly in arid areas of the Middle East to northwestern India and central Asia, in North Africa and various areas in East, West and southern Africa. The principal parasites are *Leishmania major*, transmitted mainly by *Phlebotomus papatasi*, and *Le. tropica*, transmitted by *P. sergenti*. *Leishmania major* is usually zoonotic and in most of its range gerbils (e.g. *Rhombomys opimus*) are the reservoir hosts; *Le. tropica* occurs in densely populated areas and humans appear to be the main reservoir hosts. In the New World, CL is found mainly in forests from Mexico to northern Argentina, and is caused by *Leishmania braziliensis*, *Le. amazonensis* and *Le. mexicana*. Rodents and dogs appear to be reservoir hosts. Vectors include *Lutzomyia wellcomei* and *L. flaviscutellata*.

Mucocutaneous leishmaniasis (ML) (espundia)

A severely disfiguring disease found from Mexico to Argentina. It is mainly caused by *Leishmania braziliensis*. Dogs may be reservoir hosts. *Lutzomyia wellcomei* is an important vector.

Diffuse cutaneous leishmaniasis (DCL)

A form that causes widespread cutaneous nodules or macules over the body. It is confined to Venezuela and the Dominican Republic and the highlands of Ethiopia and Kenya. In South America the parasite is *Le. amazonensis*, transmitted by *Lutzomyia flaviscutellata*, and spiny rats (*Proechimys* species) are reservoir hosts. In Ethiopia and Kenya the parasite is *Le. aethiopica*, transmitted by *Phlebotomus pedifer* and *P. longipes*, with rock hyraxes (*Procavia capensis*) as reservoir hosts.

Visceral leishmaniasis (VL)

Often referred to as ***kala-azar***. It is caused by *Leishmania donovani donovani* in most areas of its distribution, such as India, Bangladesh, Sudan, East Africa and Ethiopia. Among the vectors are *Phlebotomus argentipes* and *P. orientalis*. Rodents, wild cats and genets (*Genetta genetta*) may be reservoir hosts. In

the Mediterranean basin, Iran and central Asia, including northern and central China, *Leishmania donovani infantum* is the parasite, and the vectors include *P. ariasi* and *P. perniciosus*. Dogs and foxes (*Vulpes vulpes*) are reservoir hosts. Visceral leishmaniasis also occurs sporadically in Central and South America, where the parasite is *Le. donovani infantum* (*Le. chagasi* of some authors), transmitted by species in the *Lutzomyia longipalpis* complex.

5.3.3 Bartonellosis

Bartonellosis, sometimes called Oroya fever or Carrión's disease, is encountered in arid mountainous areas of the Andes, mainly in Peru, but also in Ecuador and Colombia. It is caused by the bacterium *Bartonella bacilliformis* and is transmitted in Peru by *Lutzomyia verrucarum* and *L. peruensis*, and by *L. colombiana* in Colombia, but there are probably other vectors. Transmission is possibly only by contamination of the mouthparts. Apart from humans there are no other vertebrate reservoir hosts.

5.3.4 Sand fly fevers

Sand flies transmit the seven viral serotypes responsible for sandfly fevers, also called papataci fever (sometimes spelt papatasi or pappataci fever), three-day fever or *Phlebotomus* fevers. The classical form of the disease is found in the Mediterranean region, but it also extends up the Nile into Egypt, and from the Middle East to northern India, Pakistan, Afghanistan and China. The most important vectors in the Old World are *P. papatasi* and *P. perniciosis*. Other forms of the virus in Central and South America are transmitted by *Lutzomyia* species such as *L. trapidoi* and *L. ylephiletor*.

Female sand flies become infective 7–10 days after taking a blood-meal. Infected females lay eggs containing the virus, and these eventually give rise to infected adults. This is an example of ***transovarial*** transmission, a phenomenon that is more common in the transmission of various tick-borne diseases (Chapters 16 and 17). There are possibly mammalian reservoir hosts, and in fact infected gerbils (*Rhombomys opimus*) have been found in Iran, but in many areas it is likely that humans are the main reservoir of infection.

Sand fly fever virus is recognized as a potential bioterrorism agent.

5.4 Control

Although phlebotomine sand flies are very susceptible to insecticides, until recently there have been few organized attempts to control them. However, in most areas where house-spraying has been used to control *Anopheles* vectors there have been large reductions in sand fly populations followed by interruption of leishmaniasis transmission. When houses in Kabul, Afghanistan, and in the Peruvian Andes were sprayed with the pyrethroid lambda-cyhalothrin, cutaneous leishmaniasis was reduced by 60% and 54% respectively. In the Americas, in countries such as Brazil and

Venezuela, spraying houses with lambda-cyhalothrin has substantially reduced the vectors of cutaneous leishmaniasis.

In areas where sand flies rest indoors, cattle sheds and chicken houses should also be sprayed. Obviously where sand flies bite and rest out of doors house-spraying will have little effect. However, if the outdoor resting sites are known (e.g. animal shelters, stone walls, tree trunks, termite hills) they can be sprayed with residual insecticides. Insecticidal fogging of outdoor resting sites may also give some, but temporary, control of vectors.

Personal protection can be achieved by applying efficient insect repellents such as DEET, piperidene-based ones and neem oil. Insecticide-impregnated bed-nets such as the long-lasting Olyset nets (see Chapter 2) will give protection from sand fly biting. For example, in Afghanistan and Syria insecticide-treated polyester bed-nets gave good protection against *Phlebotomus sergenti*, an important vector of cutaneous leishmaniasis (*Le. tropica*).

Control of sand fly larvae remains impossible, because the breeding sites of most species are unknown.

Because most leishmaniasis transmission involves ***reservoir hosts***, such as rodents and dogs, attempts have been made to destroy them. In China leishmaniasis was effectively eliminated in the 1950s by killing dogs, but although similar culls have been made in parts of Brazil and the Mediterranean region results have been disappointing. Dogs have sometimes been dipped or sprayed with pyrethroids such as deltamethrin, but repeated treatments, typically every 2–3 months, are needed. Deltamethrin-treated collars on dogs, which can remain effective for eight months, have also given good, albeit local, control of *Le. donovani infantum* in Italy and Iran. In the Mediterranean there are millions of dogs, of which 1–40% are infected with visceral leishmaniasis. Recently a new vaccine has given complete and lasting protection against leishmaniasis in dogs, thus reducing the reservoir of infection. In Russia and Jordan zoonotic cutaneous leishmaniasis has been controlled by destroying rodent colonies, but elsewhere results have not been encouraging.

Resistance to DDT was found in *P. papatasi* and *P. argentipes* in India and parts of Nepal, and greater tolerance or resistance to several insecticides, such as pyrethroids, has been reported in other sand flies.

Over 60% of visceral leishmaniasis occurs in India, Bangladesh and Nepal, and an estimated 150 million people are at risk. In 2005 these countries signed an agreement to eliminate VL by 2015, mainly based on integrated vector control.

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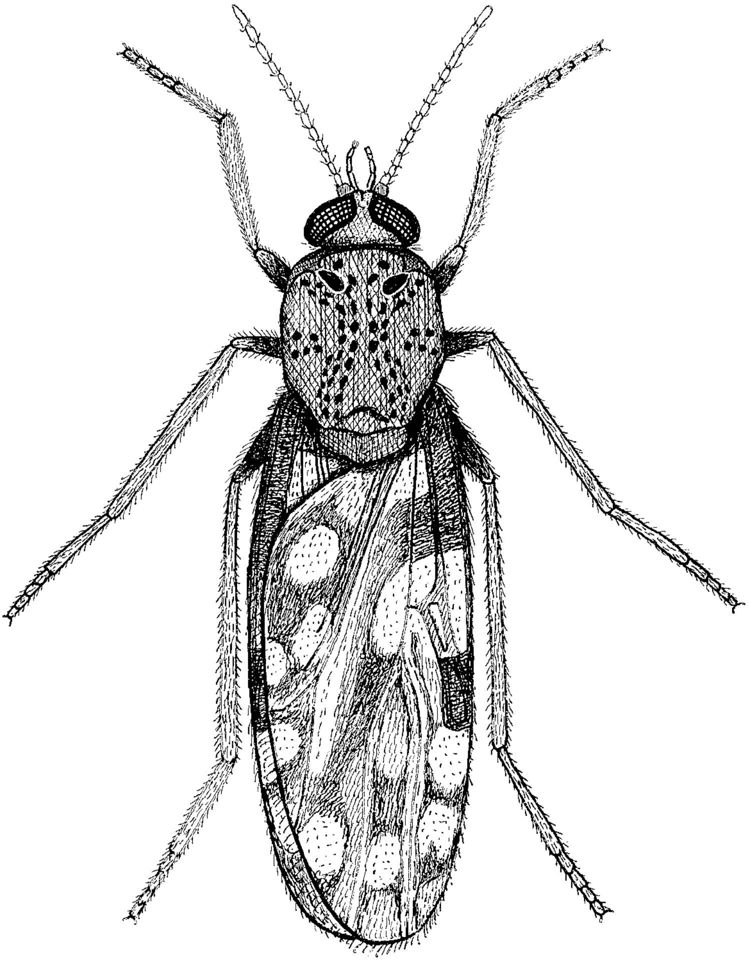
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6

Biting midges (Ceratopogonidae)



There are almost 5800 species of biting midges in about 125 genera, but only four genera have species feeding on vertebrates. Medically the most important two genera are *Leptoconops*, which is mainly found in the tropics and subtropics, including the Caribbean area and parts of the USA, and *Culicoides*, which has an almost worldwide distribution. In many parts of the world species of *Culicoides*, and in the Americas also *Leptoconops*, can constitute serious biting problems. *Culicoides* species are vectors of filarial worms, such as *Mansonella perstans* and *Mansonella streptocerca* in Africa, while *Culicoides furens* is a vector of *Mansonella ozzardi* in the Americas. All these parasites are usually regarded as non-pathogenic to humans. Although many *Leptoconops* species are biting pests they are not usually important disease vectors.

The only virus transmitted to humans by biting midges is Oropouche virus in the Americas.

Adults are sometimes known as midges or biting midges, and, especially in the Americas, as 'no-see-ums'. In Australia and some other countries they are often called sand flies, but this name is unfortunate and should be avoided because phlebotomines (Chapter 5) and occasionally simuliids (Chapter 4) may also be referred to as sand flies. The most appropriate common name is biting midges; this terminology serves to distinguish them from other small non-biting flies which are often referred to as midges.

6.1 External morphology

Adult *Culicoides* are very small, being only 1–2.5 mm long, and with the phlebotomines constitute the smallest biting flies attacking humans.

The head has a prominent pair of eyes, a pair of short five-segmented palps and a pair of relatively long filamentous antennae. As in mosquitoes, males do not take blood-meals and have feathery or ***plumose antennae***, while the ***blood-sucking females*** have ***non-plumose*** antennae. The biting mouthparts, which are very small and inconspicuous, do not project forwards but hang down from the head. The arrangement and structure of the mouthparts are very similar to those of simuliids (Chapter 4). In some species the thorax is covered dorsally with distinct very small black spots and other markings (Plate 7). In all *Culicoides* species there is dorsally on the anterior part of the thorax a pair of small elongate shiny black depressions, known as ***humeral pits***. Their presence distinguishes the genus *Culicoides* from *Leptoconops*. Wings are short and relatively broad, and apart from the first veins venation is faint.

Wings lack scales but many species are covered with minute hairs, although these are seen only under a dissecting microscope. In most *Culicoides* species the density of these hairs gives the ***wings*** the appearance of having contrasting dark and milky white spots or patches (Fig. 6.1, Plate 7).

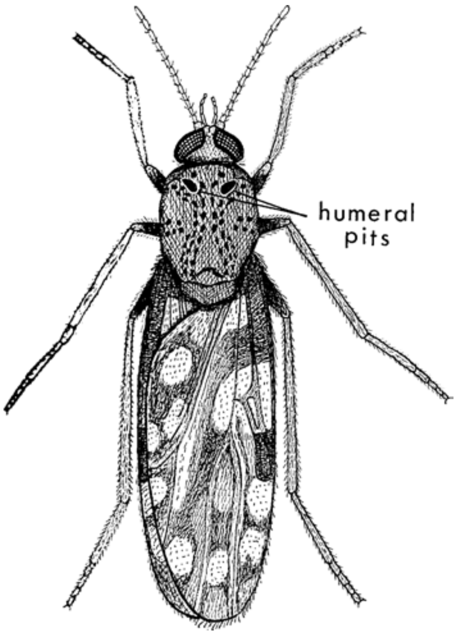


Figure 6.1 Adult *Culicoides* midge, showing patterned wings and the two thoracic humeral pits.

In life the wings are placed over the abdomen like the blades of a closed pair of scissors (Fig. 6.1). The legs are relatively short.

The abdomen is dull grey, yellowish brown or blackish, and in females is more or less rounded at its tip; in males there is a pair of small, but conspicuous, claspers.

6.2 Life cycle

Eggs are dark, cylindrical or curved and banana-shaped, and about 250–500 μm long (Fig. 6.2c). They are laid in batches of about 30–450 on the surface of mud or wet soil, especially near swamps and marshes including saltwater marshes, on decaying leaf litter, humus, manure, or on plants and other objects that are partially submerged in water. They are also laid in tree-holes, in semi-rotting vegetation and in the cut stumps of banana plants (for example *Culicoides milnei*, *C. austeni* and *C. grahamii* in Africa). The type of oviposition site selected depends on the species.

Eggs usually hatch after 2–7 days, depending on temperature and species; some temperate species overwinter as eggs. There are four larval instars, of which the fully grown larva is cylindrical, whitish, about 3–6 mm long and nematode-like. It has a small, dark (but unpigmented in *Leptoconops*) conical-shaped head followed by 12 body segments. The

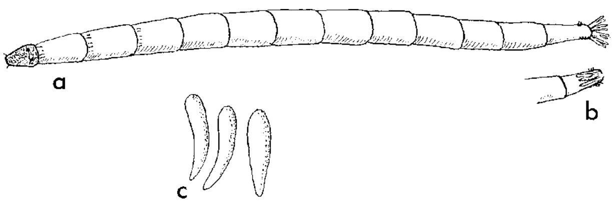


Figure 6.2 *Culicoides*: (a) larva with two four-lobed retractile papillae extending beyond the last abdominal segment; (b) last abdominal segment with papillae withdrawn into it; (c) eggs.

last segment terminates in a pair of four-lobed ***retractile papillae*** (Fig. 6.2a). These are not always readily seen in preserved larvae because they are often retracted within the last abdominal segment (Fig. 6.2b). *Culicoides* larvae are best recognized by the combination of a small dark head followed by a segmented body devoid of any obvious structures and, when they are extruded, by the presence of terminal papillae. When alive they can also be recognized by their serpentine swimming motions.

Larvae feed mainly on decaying vegetable matter. When the water level in swamps and marshes rises larvae of many species migrate to the damp soil and mud at the edges to avoid drowning. Some important pest species breed in sandy areas near the seashore. Larvae are difficult to find and are rarely encountered unless special surveys are made to collect them.

Larval development is sometimes completed within 4–5 days, but may take weeks in cooler weather, and in temperate regions many species overwinter as larvae for seven months or more. Species occupying marshy habitats frequently migrate to the drier peripheral areas for pupation. However, in species that are aquatic the pupae float at the water surface.

The pupa (Fig. 6.3) is 2–4 mm long and readily recognized by the following combination of characters: (1) a pair of respiratory trumpets on the cephalothorax which appear to be composed of two segments; (2) abdominal segments bearing small but conspicuous tubercles ending in a fine hair; and (3) a prominent pair of horn-like processes on the last abdominal segment. The pupal period usually lasts 2–3 days.

6.2.1 Adult behaviour

Adults of both sexes feed on naturally occurring sugar solutions. In addition ***females*** take blood-meals from humans and a variety of mammals and birds. Adults bite at any time of the day or night, but many species are particularly active and troublesome in the evenings. In contrast *C. grahamii*, an African species, bites mainly in the early part of the mornings. Because of their short mouthparts biting midges, unlike

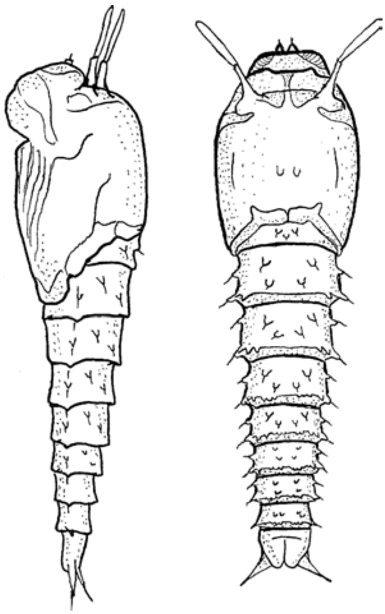


Figure 6.3 *Culicoides* pupa, lateral and dorsal views. Note the two long respiratory trumpets.

mosquitoes, tabanids and tsetse flies, can rarely bite through clothing. For this reason midges often swarm around the head, biting the face, especially the forehead and scalp. They also bite the hands and exposed arms and legs. Most species bite only outdoors, but a few, including the African species *C. milnei*, *C. austeni* and *C. grahamii*, will enter houses to feed on people (***endophagic***). About 30 species are ***autogenous***, that is they can mature and lay the first batch of eggs without a blood-meal. Adults usually fly only a few hundred metres from their larval habitats, but sometimes they are wind-dispersed considerably further. However, some species of both *Culicoides* and *Leptoconops* are known to fly 2–3 km without wind assistance. Adult females are short-lived, most probably surviving for just 1–3 weeks.

6.3 Medical importance

The Ceratopogonidae are not very important vectors of disease to humans, whereas they are of considerable veterinary importance, transmitting arboviruses such as those causing bluetongue disease in sheep and African horse sickness. They can, however, be very troublesome pests and transmit minor filarial infections as well as Oropouche virus to humans (see below).

6.3.1 Annoyance

Biting midges are very small, but what they lack in size they can make up for in numbers – as has been said, one midge is an entomological curiosity, a thousand sheer hell! In areas as dissimilar as the west coast of Scotland, the Caribbean, California and Florida, biting midges can be a serious economic threat to the tourist industry. Persistent biting of large numbers of midges can make outdoor recreational activities impossible, not only at dusk but often during much of the day. In some areas they have prevented the continuation of harvesting and other outdoor work during the evenings.

An important pest species in southern areas of North America down to Brazil is *Culicoides furens*, which breeds in salt marshes and other saline coastal habitats, while *Leptoconops torrens* and *L. bequaerti*, which breed in sandy soils and coastal areas of North America, can also be serious pests. In Peru *L. verrucarum* causes very troublesome biting problems, while in Madagascar, the Seychelles and Brunei *L. spinosifrons* is a serious biting pest. The most important *Culicoides* pest in Europe is probably *C. impunctatus*, whose larval habitats include wet heathlands, although there are many other species that can cause a nuisance.

6.3.2 Filarial infections

A few *Culicoides* species are vectors of filarial parasites to humans.

Mansonella perstans

Found in sub-Saharan Africa, especially West and Central Africa, but also occurs in parts of East Africa as far south as Zimbabwe. Vectors include *Culicoides austeni*, *C. inornatipennis*. *C. grahamii* and probably *C. milnei*. These species breed in the rotting cut stumps of banana and plantain plants. *Mansonella perstans* also occurs in Central and South America and Trinidad, where it is transmitted by other *Culicoides* species.

Mansonella streptocerca

Occurs in the rainforests of West Africa, from the Ivory Coast to Gabon, the Republic of the Congo and the Democratic Republic of the Congo, as well as western Uganda. The main vector is *C. grahamii*, but possibly also *C. milnei* and *C. austeni*. These species breed in the rotting cut stumps of banana and plantain plants.

Mansonella ozzardi

Found in Central America, such as in Mexico and Panama, in South America including Venezuela, Colombia, Brazil as far south as Argentina,

and several Caribbean islands including Trinidad and Haiti. Transmission is by *Culicoides* species, mainly *C. furens* and *C. phlebotomus*, but also by *Leptoconops becquaerti* (The role of simuliids in the transmission of this filarial parasite is discussed in Chapter 4.)

Microfilariae of all the above parasites are ***non-periodic*** and are ingested during feeding. They undergo morphological changes, invade the thoracic flight muscles, moult twice and then migrate to the head, and after about 8–12 days pass down the proboscis. Infective ***third-stage*** larvae (L_3) are deposited on the skin of the host when the female takes a blood-meal. The salivary glands of *Culicoides* play no part in the transmission of these parasites. None of these three filarial parasites appears to cause much harm and they are usually regarded as non-pathogenic, although morbidity or allergic reactions may sometimes occur.

6.3.3 Arboviruses

The only arbovirus biologically transmitted to humans by midges, as distinct from mechanical transmission, is Oropouche virus (*Bunyavirus*). This virus occurs in Columbia, Brazil, Panama, Peru and Trinidad and Tobago. Transmission is by the bite of *Culicoides paraensis*, a forest species whose immature stages are found in tree-holes. Sloths and monkeys are often infected, and they may provide a reservoir of infection for humans.

6.4 Control

It is usually very difficult to control *Culicoides* larvae, because many larval habitats are extensive, such as heathlands, freshwater and saltwater marshes and wet coastal sands, whose limits may be difficult to determine.

Although larval habitats could be eradicated by draining them or filling them in, this is usually too costly and laborious, and in many situations impractical. However, if undertaken and maintained, such methods have the advantage of giving permanent control. Although such environmental control avoids contaminating the environment with insecticides it nevertheless results in the loss of ecological habitats.

Spraying larval breeding sites with organophosphates such as malathion, diazinon or temephos has sometimes been effective, although heavy rainfall is often required to wash the insecticide through surface vegetation to the underlying soil and mud harbouring the larvae. Spraying may require repeating after 1–2 months, and increased public awareness of environmental contamination might prevent this approach.

A few species enter buildings to bite, and bed-nets and screening used to exclude house flies and mosquitoes will not keep out the much smaller midges, unless nets are impregnated with pyrethroids such as permethrin

and deltamethrin. Such treated nets may remain effective for six months, or for five years if long-lasting Olyset nets are used. (For more details on the use of insecticide-impregnated bed-nets against vectors see Chapter 2.)

Insecticidal fogs or ultra-low-volume (ULV) applications have sometimes been used to kill adults resting in vegetation, but the effects are very short-lived and sprayed areas are soon invaded by midges flying in from unsprayed areas.

Limited personal protection can be achieved by using repellents such as DEET.

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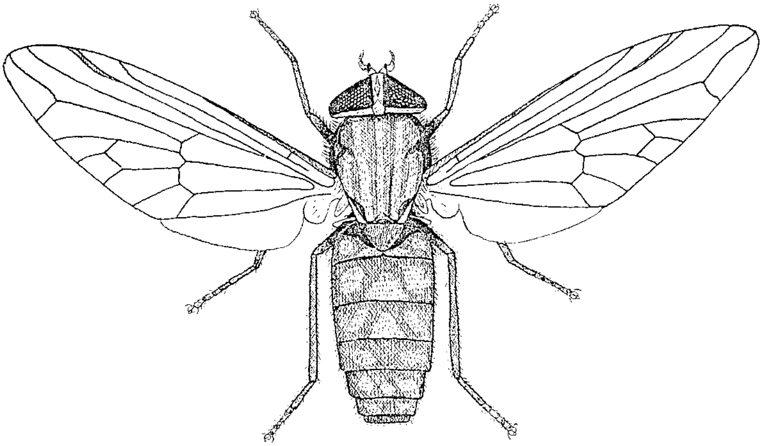
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7

Horse flies (Tabanidae)



Tabanids are large biting flies generally called horse flies, although other vernacular names include greenheads (some species of *Tabanus*), clegs and stouts (*Haematopota*) and deer flies (*Chrysops*). All belong to the family Tabanidae, which comprises about 4300 species and subspecies in 133 genera. Medically the most important are species of *Tabanus*, *Chrysops* and *Haematopota*. Tabanids have been incriminated in the spread of anthrax and tularaemia and might be involved in the transmission of Lyme disease (usually transmitted by hard ticks), but this remains unclear. But their main medical importance is that species of *Chrysops*, mainly *C. silaceus* and *C. dimidiatus*, are vectors in West and Central Africa of the filarial worm *Loa loa*.

The Tabanidae have a worldwide distribution. Species of *Tabanus* and *Chrysops* are found in temperate and tropical areas, but *Haematopota* is absent from South America and Australasia and is uncommon in North America.

7.1 External morphology

A generalized description is presented of the Tabanidae, with special reference to the genera *Chrysops*, *Tabanus* and *Haematopota*.

Tabanids are medium to very large flies (6–30 mm long). Many, especially *Tabanus* species, are robust and heavily built, and this genus contains the largest biting flies, some with a wingspan of 65 mm. The colouration of tabanids varies from very dark brown or black to lighter reddish brown, yellow or greenish; frequently the abdomen and thorax have stripes or patches of contrasting colours (Fig. 7.1). The head is large and, viewed from above, is more or less ***semicircular*** (Fig. 7.2); it is often described as semilunar. The head has a conspicuous pair of compound eyes which in life may be marked with contrasting ***iridescent*** colours, such as greens and reds or even purplish hues, arranged in bands, zigzags or spots. Adults are ***sexed*** by examining their eyes. In the female there is a distinct space on top of the head separating the eyes: this is known as a ***dichoptic*** condition (Fig. 7.2a). In females of some species this space between the eyes may be narrow, whereas in others, especially *Chrysops*, it is quite large. In males the eyes are so large that they occupy almost all of the head and either touch each other on top of the head or are very narrowly separated, this being known as a ***holoptic*** condition (Fig. 7.2b).

The ***antennae*** are relatively small but stout. They consist of three segments; the last is subdivided into usually three or four small divisions by annulations. Unlike the Muscidae, Glossinidae and Calliphoridae, there is no antennal arista. The size and shape of the antennae serve to distinguish the genera *Chrysops*, *Haematopota* and *Tabanus* (Fig. 7.3). The mouthparts of female Tabanidae are stout and adapted for biting and, unlike those of tsetse flies, mosquitoes and *Stomoxys*, they do not project forwards but hang down from the head. Only ***female*** tabanids take blood-meals.

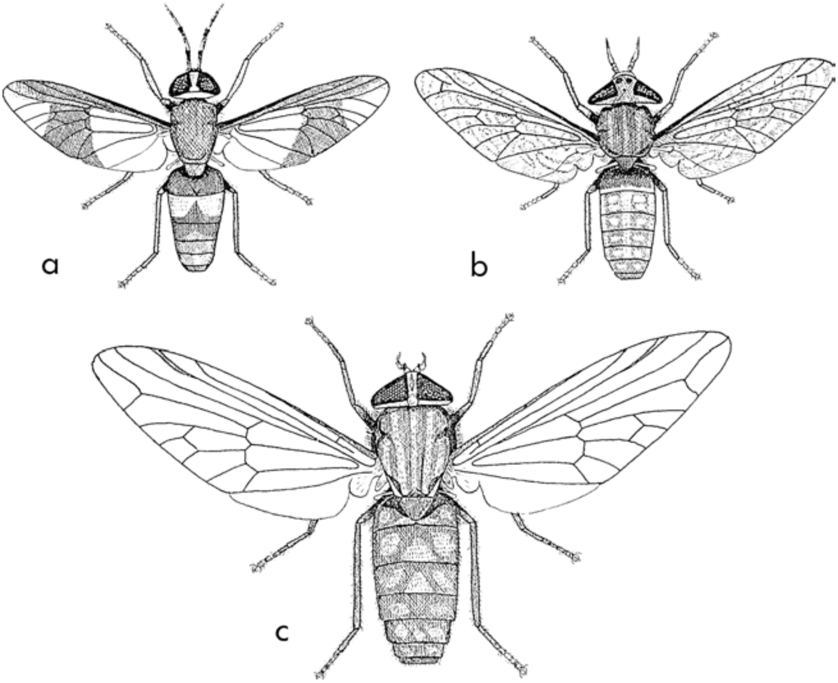


Figure 7.1 Adult female tabanids belonging to three genera: (a) *Chrysops*; (b) *Haematopota*; (c) *Tabanus*.

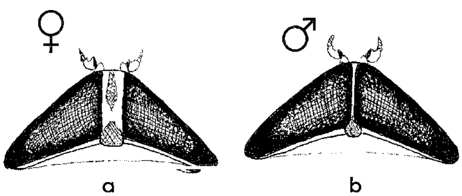


Figure 7.2 Dorsal view of tabanid heads: (a) female showing dichoptic eyes; (b) male with holoptic eyes.

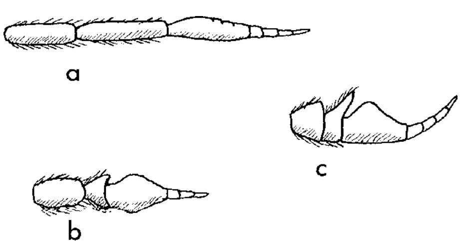


Figure 7.3 Antennae of adult tabanids belonging to three genera: (a) *Chrysops*; (b) *Haematopota*; (c) *Tabanus*.

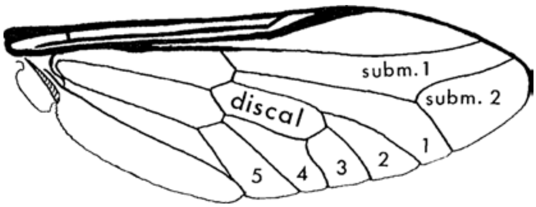


Figure 7.4 Wing of an adult tabanid, showing discal cell, two submarginal cells (subm.) and five posterior cells (1–5).

The stout thorax bears a pair of wings which have two submarginal and five posterior cells and a completely closed ***discal cell*** in approximately the centre of the wing (Fig. 7.4). Although wing venation alone may not be sufficient to identify the Tabanidae from all other Diptera, it nevertheless serves as a useful guide when considered with other characters, such as the shape and structure of the antennae and biting mouthparts. Wings may be completely clear and devoid of colour, have areas of brown colouration, be distinctly banded, or appear mottled or speckled due to greyish patches (Fig. 7.1). Adults at rest have the wings placed either like a pair of open scissors over the abdomen or at a roof-like angle completely obscuring the abdomen. The presence or absence of coloured areas on the wings and how they are held over the body provides useful additional characters for distinguishing between *Chrysops*, *Tabanus* and *Haematopota* (see below).

The abdomen is usually broad and stout, and in unfed flies characteristically flattened dorsoventrally. It may be a more or less uniformly dark brown, blackish, light brown, reddish brown, yellowish or even greenish, or alternatively marked with contrasting coloured stripes or patches.

7.1.1 Identification of adult *Chrysops*, *Tabanus* and *Haematopota*

Chrysops species (deer flies)

Chrysops species (Plate 8) are medium-sized flies about 6–12 mm long. In life most species have ***iridescent*** eyes, commonly with spots of red, green or purple. The wings are held partially over the abdomen in an open scissor-like fashion, and usually have one or more brownish transverse bands (Fig. 7.1a). In many species the abdomen is blackish with orange or yellow patches or bands.

The most reliable method of distinguishing *Chrysops* from *Tabanus* and *Haematopota* is by their ***antennae***. In *Chrysops* the second segment of the antenna is long and cylindrical and lacks any projection (Fig. 7.3a), while the third segment has four small subdivisions. The hind tibiae have apical spurs which are absent in *Tabanus* and *Haematopota*.

Chrysops has a worldwide distribution.

Tabanus species (horse flies, greenheads)

Tabanus species are medium to very large flies, 10–30 mm long. Their ***eyes*** are frequently brownish but may be iridescent, with markings usually in the form of horizontal bands. Their wings, which are held over the body much as in *Chrysops*, are often clear (Fig. 7.1c), but in some species they have dark markings.

Tabanus species are readily identified by the shape and size of the ***antennae***. Both the second and third antennal segments have small but distinct projections dorsally (Fig. 7.3c), while the third segment has four small subdivisions and is usually distinctly curved upwards. The antennae are much shorter than those of *Chrysops* species, and are therefore less conspicuous.

Tabanus has a worldwide distribution.

Haematopota species (clegs, stouts)

Haematopota species are dark grey medium-sized flies, about 8–25 mm long, which are easily distinguished from *Tabanus* and *Chrysops* because in life the wings are folded ***roof-like*** over the abdomen. Moreover, in nearly all species the wings are ***dusty grey*** and speckled or mottled (Fig. 7.1b, Plate 9), The ***eyes*** have zigzag bands of iridescent colours. Antennae are rather similar to those of *Tabanus* but are usually a little longer. The third segment is straight, not curved as in *Tabanus*, has only three, not four, small subdivisions and does not bear a dorsal projection (Fig. 7.3b).

Haematopota species are not found in South America or Australasia, and only five species occur in North America. They are, however, common in Europe, Asia, Africa and the Far East.

7.2 Life cycle

Both males and females feed on naturally occurring sugary secretions, but in addition ***females*** bite a wide variety of mammals including humans, domesticated animals, especially horses and cattle, deer and many other herbivores, as well as carnivores and monkeys. A few species attack birds.

Oviposition sites overhang, or are adjacent to, the larval habitats, which are often muddy, aquatic or semi-aquatic (see page 121). Some 100–1000 eggs, the number depending on the species, are firmly glued in an upright position in a single large mass (up to 25 mm long) on the underside of objects such as leaves, grassy vegetation, twigs, small branches, stones and rocks. They are covered with a secretion that makes them waterproof and are often arranged in a more or less lozenge-shaped pattern (Fig. 7.5a). Eggs are whitish when laid but soon darken to a greyish or blackish colour; they are 1–3 mm long, and curved or approximately cigar-shaped. They usually hatch after 5–14 days, the time depending on both temperature and

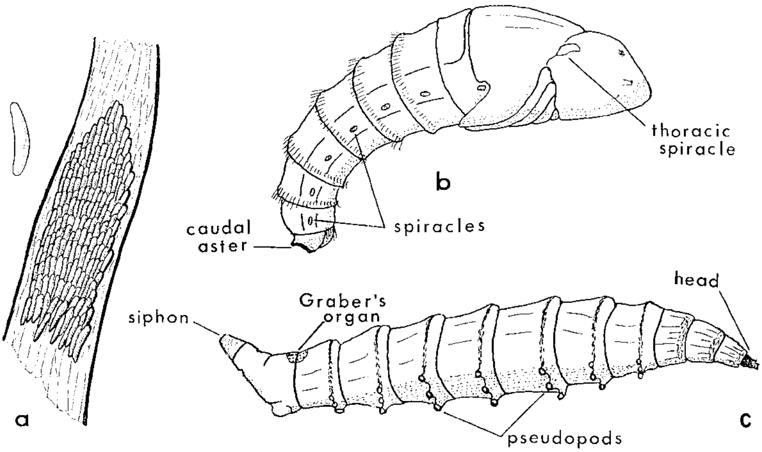


Figure 7.5 Immature stages of tabanids: (a) single egg and egg mass glued to a piece of grass; (b) pupa; (c) larva.

species. After wriggling out of the eggs the young larvae drop down onto the underlying mud or water.

Larvae are cylindrical and rather pointed at both ends (Fig. 7.5c). They are creamy white, brown or even greenish but often have darkish pigmentation near the borders of the segments. The very small black head can be retracted into the thorax. There are 11–12 well-differentiated body segments. Larvae are readily recognized by the prominent raised ***tyre-like rings*** which encircle most body segments. The first seven abdominal segments have one pair of lateral and two pairs of ventral (a total of six) conspicuous roundish protuberances called ***pseudopods***. The presence of prominent rings and these pseudopods readily identify larvae of tabanids. The last abdominal segment has dorsally a short ***siphon*** which can be retracted into the abdomen, and a pear-shaped structure known as Graber's organ, which is composed of 15 or fewer black globular bodies. The exact function of this organ is unclear.

Larvae live in mud, rotting vegetation, damp soil, in shallow and often muddy waters, at the edges of small pools, swamps, ditches or slowly flowing streams. In aquatic habitats larvae sometimes adhere to floating leaves, logs or other debris. A few species breed in tree-holes and others in brackish habitats. Larvae of certain *Tabanus* and *Haematopota* species, however, occur in drier soils of pastures and in the ground near the bases of trees. Larvae breathe through their abdominal short siphon, and because they are poor swimmers aquatic species are usually found only in shallow waters. They move rather sluggishly in their muddy, aquatic or semi-aquatic habitats. Larvae of *Tabanus* and *Haematopota* are predaceous or cannibalistic. Carnivorous larvae inject a venom into their prey and occasionally cause considerable pain by biting people working barefoot in

ricefields. In some species, in particular *Chrysops*, larvae are mainly scavengers, feeding on detritus and a variety of dead and decaying vegetable and animal matter.

Larval development is of a ***long duration***. In both temperate and tropical countries many species remain as larvae for 1–2 years, and several cold-temperate species have a larval period of 3 years or even more. Relatively little is known about their life cycle, but there appear to be 6–13 larval instars. Depending upon the species, mature larvae may be 10–60 mm long.

Prior to pupation mature larvae migrate to drier areas at the periphery of larval habitats, where they pupate. The pupa is partially buried in the mud or soil in an upright position and, superficially, looks like a chrysalis of a butterfly (Fig. 7.5b). It is 6–35 mm long, the size depending on the species, and distinctly curved and usually brown. The head and thorax are combined to form a distinct cephalothorax which has a pair of lateral and relatively large ear-shaped spiracles. The abdomen has eight well-defined segments; the first seven have a pair of lateral spiracles, and segments 2–7 have an encircling row of small backwardly directed spines. The short terminal eighth abdominal segment is provided with six lobes which bear spine-like processes, known collectively as the ***caudal aster***. The pupal period lasts about 5–20 days.

7.2.1 Adult behaviour

Females of most species feed during the ***daytime*** and are especially active in bright sunshine, although a few species are crepuscular and some feed at night. The amount of blood ingested by *Chrysops* species is about 20–25 mg, whereas larger flies such as *Tabanus* species may take up to 100–500 mg of blood. Adults locate their hosts mainly by sight, although olfactory stimuli such as carbon dioxide and other host odours also play a role in host location. Tabanids are powerful fliers and may disperse several kilometres.

Most tabanids inhabit woods and forests. Many *Chrysops* species are common in low-lying marshy scrub areas or swampy woods; some species, however, are found in more open savanna and grassland areas. Adults do not usually enter houses to feed, but *C. silaceus* in Africa is an exception. It is also attracted by smoke from wood burning and from forest fires.

Because of their large and blade-like mouthparts, bites are painful and wounds inflicted by tabanids frequently continue to bleed after the female has departed. Because of their painful bites tabanids are frequently disturbed when feeding, and several small blood-meals may be taken from the same or different hosts before the female has obtained a complete meal. Such interrupted feeding increases their likelihood of being mechanical vectors of disease. Because of their attraction to dark objects they often bite through coloured clothing when attacking Caucasians rather than biting exposed areas of pale skin; in this respect they behave like tsetse flies.

In both temperate and tropical areas the occurrence of adults is seasonal. In temperate countries adults usually die off at the end of the summer and a new population emerges in the following spring or summer. In the tropics tabanids may not completely disappear in the dry months, but their numbers are normally much reduced. Maximum numbers of biting flies usually appear towards the beginning of the rainy season.

7.3 Medical importance

7.3.1 Minor infections

Because of their painful bites, tabanids may sometimes be troublesome pests and can make outdoor activities, whether recreational or work, difficult. People can develop severe allergic symptoms due to the large amount of saliva that is pumped into bite wounds to prevent blood-clotting.

Because females tend to be intermittent feeders, and are often disturbed during feeding, tabanids are particularly liable to be mechanical vectors, and in this way can spread anthrax (*Bacillus anthracis*). In North America and Russia they have been incriminated in the mechanical spread of tularaemia (*Francisella tularensis*) from horses, rabbits and rodents to humans. *Chrysops discalis* has been identified as a vector of tularaemia in North America, but other tabanid species are most likely involved. The disease is also commonly spread by handling infected rodents, by ixodid tick bites, and by eating insufficiently cooked meat. Lyme disease (*Borrelia burgdorferi*), which is normally transmitted by ixodid ticks, may possibly be transmitted mechanically by tabanids. They can also mechanically transmit *Trypanosoma vivax*, causing trypanosomiasis in cattle in Africa and Latin America.

Tabanids transmit viruses, bacteria, protozoa and filarial worms to livestock and therefore are of veterinary importance.

7.3.2 Loiasis

The only important and cyclically transmitted disease spread to humans by tabanids is loiasis, caused by the nematode *Loa loa*, which undergoes a developmental cycle in the fly. This disease occurs principally in the equatorial rainforests of Ghana across to Nigeria and Cameroon, Equatorial Guinea, Gabon, the Republic of the Congo, the Democratic Republic of the Congo, northern Angola, southern Sudan and into western parts of Uganda. The ***diurnally periodic*** microfilariae are more or less absent from peripheral blood of people at night but appear in it during the day, especially in the morning. The microfilariae are therefore readily picked up by *Chrysops silaceus* and *C. dimidiatus*, species which bite during the day. In areas of Africa such as in Bahr-el-Ghazal, Sudan, where these flies are absent, other species, such as *C. distinctipennis* and *C. longicornis*, appear to be vectors.

After an infective blood-meal many, but not all, ingested microfilariae survive the process of blood digestion, penetrate the gut wall and migrate to the abdomen, and to a lesser extent the thorax and head. Here they moult twice and develop into ***third-stage*** larvae (L_3) (2 mm long), which migrate to the thorax and head, and after 7–15 days congregate in the proboscis. When *Chrysops* feed on humans as many as 200 L_3 larvae may be deposited on the skin. Most die, but some manage to pass through the punctures made by the biting flies, or through skin abrasions, and enter the host. They migrate to the connective tissues and become mature worms in three months, and after a further three months microfilariae appear in the peripheral blood. Adult worms migrate through connective tissue in any part of the body; occasionally they pass across the conjunctiva, and understandably this can cause alarm in the patient! Migrating worms passing through the body can cause allergic reactions resulting in swellings which are known as ***Calabar swellings***, which after a few days disappear to reappear elsewhere.

A related form of *Loa loa*, namely *L. loa papionis*, has been found in monkeys. The microfilariae appear in their peripheral blood at night and are picked up by *C. centurionis* and *C. langi*, species which are mainly crepuscular and nocturnal and which feed in the tree canopy, where monkeys are sleeping. However, laboratory experiments suggest that transmission of *L. loa papionis* from monkeys to humans is unlikely.

7.4 Control

There are very few practical measures to control tabanids. Efficient drainage of larval habitats might reduce adult production, but problems of locating often extensive larval habitats and the cost of drainage usually prevent this approach. Because of difficulties of locating larval habitats, larviciding, such as with insecticides, is usually logistically impossible.

Some level of local control can sometimes be achieved by space spraying with pyrethroids to kill adult flies, but realistically there is usually no easy and efficient way of controlling *Chrysops* species. However, some degree of local protection may be obtained with insect repellents.

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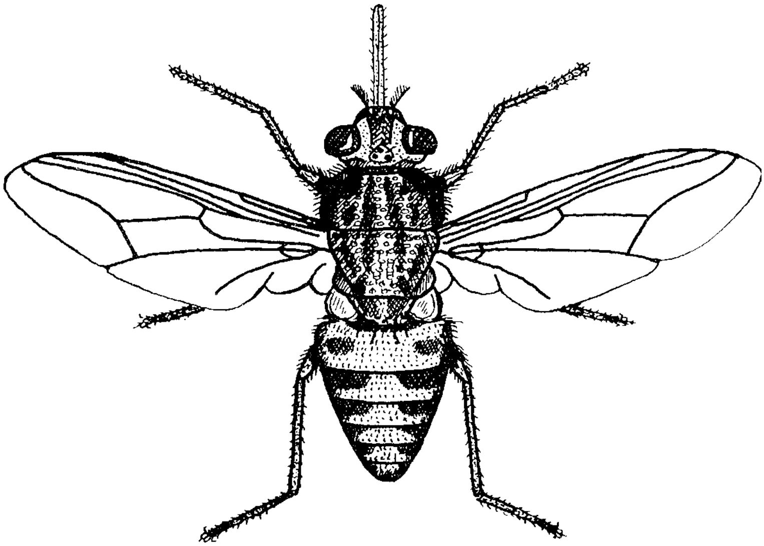
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8

Tsetse flies (Glossinidae)



There are 31 species and subspecies of tsetse flies, but the actual number depends on how many forms are recognized as subspecies. All tsetse flies belong to the genus *Glossina*, the only genus in the family Glossinidae. Apart from two species found in southwest Arabia, tsetse flies are restricted to sub-Saharan Africa from approximately latitude 10° north to 20° south, but extending to 30° south along the eastern coastal area. Some species, such as *Glossina morsitans*, are found across West Africa to Central and East Africa, whereas others are more restricted in their distribution. For example, *G. palpalis* occurs only in the West African subregion.

Tsetse flies are vectors of both human and animal African trypanosomiasis, the disease in humans being called sleeping sickness. The most important vectors are *G. palpalis*, *G. tachinoides*, *G. fuscipes*, *G. pallidipes* and *G. morsitans*.

8.1 External morphology

A general description of tsetse flies, without special reference to any particular species, is as follows. Adults are yellowish or brown-black robust flies that are rather larger (6–14 mm) than house flies. Some species have the abdominal segments uniformly coloured, whereas others may have lighter-coloured transverse stripes and a median longitudinal one. Tsetse flies are distinguished from other flies by the combination of (1) a rigid forward-projecting ***proboscis*** and (2) a closed cell between wing veins 4 and 5 which, with a little imagination, looks like an upside-down hatchet (i.e. axe, cleaver or chopper) and consequently is often termed the ***hatchet cell*** (Figs. 8.1b, 8.2a, Plate 10). The hatchet cell serves to conclusively identify a tsetse fly. At rest tsetse flies also differ from most flies in having the ***wings*** placed over the abdomen like the closed blades of a pair of scissors (Fig. 8.1a).

The proboscis is long, with a bulbous base, and points forwards from the head (Fig. 8.1c). When a tsetse fly feeds, saliva containing anticoagulants is pumped down into the wound formed by the fly. A long pair of palps occur dorsally, very close to the proboscis, and lie alongside it. They are difficult to distinguish except when the tsetse fly is feeding and the proboscis is swung downwards while the palps remain projecting forwards (Fig. 8.2b). The first two antennal segments are small and inconspicuous but the third is relatively large, cylindrical and somewhat banana-shaped. Near its base is the arista, which has branched hairs, but only on the upper surface (Fig. 8.2c).

Dorsally the thorax has dark brown stripes or patches. There are eight abdominal segments, which may be uniformly dark brown or blackish, or have pale brown or yellowish transverse stripes. Because ***both sexes*** take blood-meals and can be disease vectors it is not important to distinguish them; nevertheless tsetse flies can be sexed by examining the tip of the

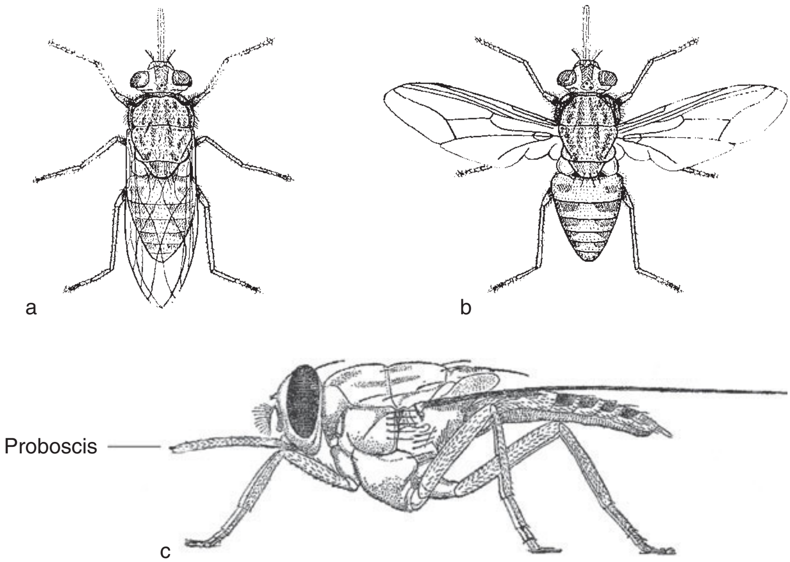


Figure 8.1 Tsetse flies: (a) wings folded over the body like a pair of closed scissors; (b) wings purposely spread out to display abdomen and wing venation; (c) side view.

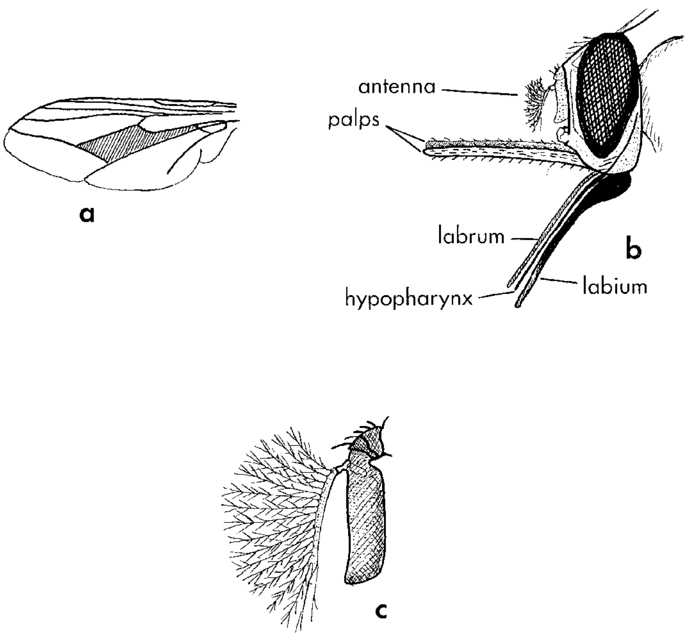


Figure 8.2 Adult tsetse fly: (a) wing, showing the hatchet cell identified by shading; (b) lateral view of head, showing mouthparts, antenna and palps; (c) antenna, showing plumose branching of hairs on upper side of the arista.

abdomen. In the males there is ventrally a prominent raised button-like structure called the hypopygium, which when unfolded reveals a pair of genital claspers. In the female fly there is no such button-like protuberance.

8.1.1 Alimentary canal of the adult fly

Knowing the morphology of the alimentary canal and associated salivary glands (Fig. 8.3) is essential for understanding the life cycle of trypanosomes in the tsetse fly.

The food channel in the proboscis leads to the pharynx and then the oesophagus, which has a slender duct leading to the oesophageal diverticulum, commonly called the crop. Just behind the oesophagus is a bulbous structure termed the ***proventriculus***. The distal end of the proventriculus marks the end of the fore-gut and beginning of the mid-gut, which in tsetse flies is very long and convoluted. The ***peritrophic membrane*** is secreted by epithelial cells in the anterior part of the proventriculus and has an important role in the cyclical development of sleeping sickness trypanosomes in the tsetse fly. When first produced, the peritrophic membrane is very delicate, soft and almost fluid, but as it passes through the gut it hardens to form a thin but relatively tough sleeve which lines the entire length of the mid-gut.

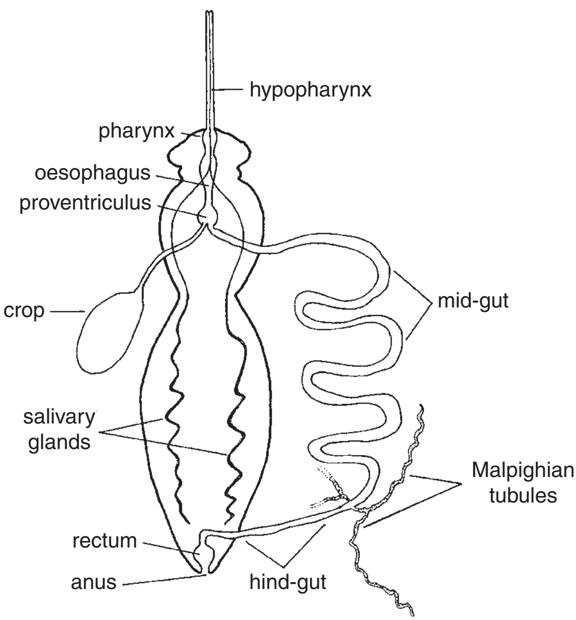


Figure 8.3 Adult tsetse fly, dissected to show diagrammatically the alimentary canal and paired thread-like salivary glands.

The junction of the four Malpighian tubules separates the mid-gut from the hind-gut.

The thread-like paired salivary glands originating in the head of a tsetse fly are enormously long, very convoluted and stretch back almost to the end of the abdomen. Anteriorly, ducts from both glands unite in the head to form the common salivary duct; this passes through the hypopharynx, which runs down the centre of the proboscis.

8.2 Life cycle

8.2.1 Feeding and reproduction

Both ***male and female*** tsetse flies bite people, a large variety of domesticated and wild mammals, and sometimes reptiles and birds. No species of tsetse feeds exclusively on one type of host although most show definite host preferences, often associated with host availability. For example, in East Africa *Glossina swynnertoni* feeds mainly on wild pigs and *G. morsitans* on wild and domesticated bovids as well as on wild pigs, whereas in West Africa *G. morsitans* feeds mainly on warthogs (*Phacochoerus africanus*). In East Africa *G. pallidipes* feeds principally on wild bovids, while in West Africa *G. palpalis* feeds predominantly on reptiles and humans, and in West Africa *G. tachinoides* feeds on humans and bovids, but in southern Nigeria it feeds predominantly on domestic pigs. Tsetse flies blood-feed about every 2–3 days, although in cool humid conditions it may be about every 10 days. Feeding is restricted to the daytime, and vision, as well as olfactory cues emanating from host breath and urine, is important in host location, dark moving objects being particularly attractive. On pale-skinned people, such as Caucasians, tsetse flies often bite through dark clothing such as socks, trousers and shorts in preference to settling on the skin. During feeding blood sucked up the proboscis passes to the crop and later to the mid-gut, where digestion proceeds.

The different types of flies so far described in this book lay eggs; in marked contrast tsetse flies do not, but instead they deposit larvae, one at a time (i.e. they are ***larviparous***). Adults of *Sarcophaga* and *Wohlfahrtia* also deposit larvae, not eggs (Chapter 10).

After females have mated and taken a blood-meal a single egg in one of the two ovaries completes maturation. It then passes down the common oviduct into the uterus, where it is fertilized by sperm from the paired spermathecae. The egg hatches within the uterus after about 3–4 days. The uterus is supplied with a conspicuous pair of branched secretory glands called ***milk glands*** (Fig. 8.4). Secretions from these glands provide the larva with all the food it needs for growth and development. The larva passes through three instars in the female. Regular blood-meals must be taken for a continuous and adequate provision of nutrient fluid from the milk

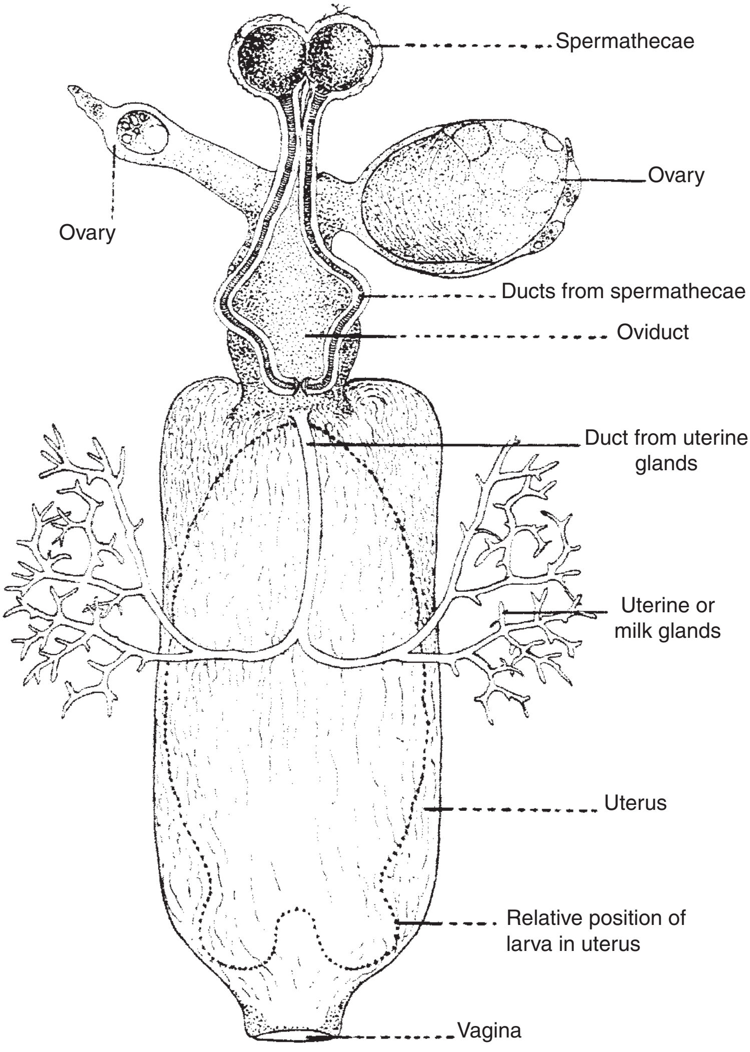


Figure 8.4 Diagrammatic representation of the female reproductive system of a tsetse fly, showing position of a larva in the uterus.

glands. If the fly is unable to feed, the larva may fail to complete its development and as a consequence be 'aborted'.

Larval development takes about 9 days, by which time the third- and final-instar larva is 5–7 mm long. It is creamy white and composed of 12 visible segments, the last of which bears a pair of prominent dark protuberances called the ***polypneustic lobes*** (Fig. 8.5a), which are respiratory structures. A female containing a fully developed larva is easily recognized because the fly's abdomen is enlarged and stretched, i.e. the fly is obviously

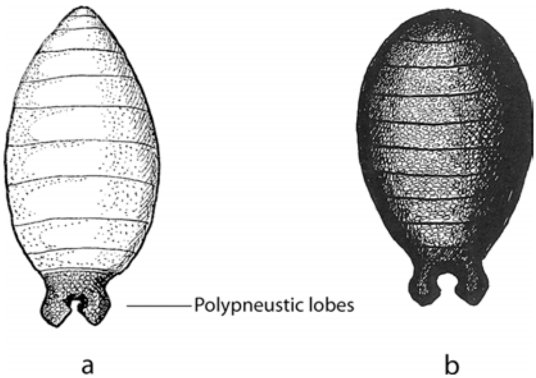


Figure 8.5 Tsetse fly: (a) larva: (b) puparium.

'pregnant'. Furthermore, the black larval polypneustic lobes can be seen through her abdominal integument.

The mature third-instar larva wriggles out, posterior end first, from the genital orifice; thus birth can be termed a 'breech case'. Females select shaded sites for larviposition. The larva is deposited on loose friable soil, sand or humus, frequently underneath bushes, trees, logs, rocks, between buttress-roots of trees, in sandy riverbeds, in animal burrows and even in rot-holes in trees which may be 4–5 m above the ground. Immediately after the larva is deposited it commences to bury itself under 2–5 cm of soil. After about 15 minutes the third-instar larval skin contracts and hardens to form a reddish brown or dark brown barrel-shaped ***puparium*** which measures about 5–8 mm, and has, like the larva, distinct polypneustic lobes (Fig. 8.5b). Within this puparial case the larva pupates.

Duration of the puparial period is comparatively long, usually 4–5 weeks, but at high temperatures (30 °C) it may be completed within 3 weeks, and conversely at low temperatures (20 °C) prolonged to 7 weeks. After completion of puparial development the fly emerges from the puparium, forces its way to the surface of the ground and flies away.

During larval development in the female the tsetse fly feeds every 2–3 days. The first larva is deposited about 16–20 days after the female has emerged from the puparium; thereafter, if food is plentiful, a larva is deposited about every 9–12 days. In the laboratory female tsetse flies have produced up to 20 offspring, but the average is nearer 5–8. Breeding generally continues throughout the year, but in very humid conditions reproduction may be diminished. Maximum population size is usually reached at the end of the rainy season. The population diminishes in the dry season, when suitable areas of refuge for adult flies and suitable larviposition sites may become restricted and localized.

8.2.2 Adult behaviour

Knowledge of the behaviour of tsetse flies is essential for understanding their role in the transmission of sleeping sickness, and for the development of effective control strategies.

Blood-engorged tsetse flies, and unfed hungry flies waiting to feed, spend the night and much of the day resting in dark and usually humid sites. In fact tsetse flies spend about ***23 hours*** a day resting on vegetation. During the day favoured resting sites of most species are twigs, branches and trunks of trees and bushes. Flies are not found resting in sites having temperatures above about 36 °C. At night tsetse flies rest mainly on the upper surfaces of leaves. Accurate knowledge of resting sites may be required for control measures. For example, the height at which adults rest on trees determines the height at which they need to be sprayed with insecticides. Most species in fact rest below 4 m; in Nigeria 50% of *G. palpalis* and *G. morsitans* commonly rest between ground level and 30 cm.

Based on their morphology, ecology, karyotype and behaviour, tsetse flies can be separated into the following three main groups.

Fusca group (forest flies)

The *fusca* group contains 15 species and subspecies of *Glossina*, all of which are large flies (10.5–15.5 mm). They are forest flies (except *G. longipennis*, which occurs in arid areas of East Africa) and most are restricted to the equatorial forests of West and western Central Africa. For example, *G. fusca* occurs mainly in relict forests of West and Central Africa, whereas *G. brevipalpis* is found in secondary forests of East Africa.

The *fusca* group rarely feeds on people, and none of the species is a vector of sleeping sickness.

Morsitans group (savanna flies)

Seven species and subspecies are included within the *morsitans* group. They are medium-sized insects, 7.5–11 mm long, and typically inhabit savanna regions of Africa, which may extend from the coast, or the edges of forests, to dry semi-desert regions. *Glossina morsitans* occupies the savanna regions of West, Central and East Africa, whereas *G. pallidipes* is found in savannas of East Africa and parts of southern Africa, and *G. swynnertoni* is restricted to the savannas of a very limited area of East Africa. Within savannas *G. morsitans* and *G. pallidipes* occur in areas ranging from wooded sites at the edges of forests to dry thicket vegetation of arid zones, whereas *G. swynnertoni* is restricted mainly to relatively dry thicket country.

All three species mentioned above are vectors of sleeping sickness. The most important is *G. morsitans*, although this species is not a vector in West Africa.

Palpalis group (riverine and forest flies)

Nine tsetse species and subspecies are included in the *palpalis* group, the smallest being about 6.5 mm in length and the largest 11 mm. They are essentially flies inhabiting wetter types of vegetation, such as forests, luxuriant scrub and vegetation growing along rivers and shores of lakes. *Glossina palpalis* inhabits riverine vegetation bordering rivers and lakes, mangrove swamps and forested areas, and occurs throughout most of West Africa, down the western part of the continent to Angola. *Glossina fuscipes*, which is closely related to *G. palpalis*, occurs mainly in Central Africa but extends its range to the western areas of East Africa. *Glossina tachinoides* is a riverine species found near streams and rivers in wet humid coastal areas, through wooded savanna regions to the riverine vegetation of very dry savanna areas. It is found mainly in West and Central Africa but also occurs in parts of Ethiopia and Sudan. All these species are vectors of sleeping sickness.

8.3 Medical importance

All *Glossina* species are potential vectors of African trypanosomiasis to humans. However, relatively few species of tsetse flies are natural vectors because many species rarely, if ever, feed on people. It is the behaviour of adult tsetse flies and the degree of fly–human contact, and in the case of Rhodesian sleeping sickness also the degree of vector contact with reservoir hosts of the trypanosomes, that establishes whether a tsetse fly is a vector.

Sleeping sickness has a patchy distribution over about 10^6 km^2 of land (that is an area greater than the USA) in 36 African countries. A few years ago an estimated 30 000 new cases were recorded annually, and the WHO estimated there were probably about 400 000 new cases a year and 55 000 deaths. However, in 2009 the reported cases were below 10 000 for the first time in 50 years, due, it is claimed, to control efforts. Presently many countries are reporting just 100–1000 new cases a year.

There are two subspecies of trypanosomes causing sleeping sickness in humans, namely *Trypanosoma brucei gambiense* and *T. brucei rhodesiense*. *Trypanosoma b. gambiensis* accounts for 95% of reported cases of sleeping sickness. These parasites are morphologically indistinguishable but produce different clinical symptoms and have different epidemiologies. The most important vectors of sleeping sickness are *G. palpalis*, *G. fuscipes*, *G. tachinoides*, *G. morsitans* and *G. pallidipes*.

The developmental cycle of *T. brucei gambiense* and *T. brucei rhodesiense* in the tsetse fly is the same, and is as follows. Trypanosomes in the blood are sucked up by male and female tsetse flies during blood-feeding from an infected person (or, particularly in the case of *T. brucei rhodesiense*, often from a non-human reservoir host). They pass through the oesophagus to the crop, and then, after feeding has ceased, into the ***peritrophic tube*** lining the mid-

gut. About 9–11 days after feeding the trypanosomes penetrate the middle section of the peritrophic membrane and pass across into the space between the membrane and the gut, called the ***ectoperitrophic space***. Here they multiply, and after 3–9 days the parasites penetrate the anterior softer part of the peritrophic membrane and migrate to the ***proventriculus***. From here they pass down the food channel in the proboscis and pass up the hypopharynx or salivary duct to invade the ***salivary glands***, where they develop into ***epimastigotes*** and multiply enormously. About 18–35 days after an infective blood-meal the tsetse fly becomes infective, and metacyclic ***trypomastigotes*** (metatrypanosomes) are injected into a vertebrate host when the fly feeds. It seems that sometimes parasites may take a more direct route in which they pass through the peritrophic membrane and gut wall to enter the haemocoel (body cavity) and then invade the salivary glands.

When determining mature infection rates in tsetse flies by dissection, any trypanosomes found in the gut or proboscis are ignored, as only those in the salivary glands can be *T. brucei gambiense* or *T. brucei rhodesiense* infections, although immature forms occur elsewhere. There are complications, because *T. brucei brucei*, which does not cause sleeping sickness in humans but causes an animal trypanosomiasis commonly called nagana, undergoes a similar cyclical development in the fly. Consequently, the presence of trypomastigotes (metacyclic forms) in the salivary glands does not necessarily indicate the presence of trypanosomes infective to people.

Salivary gland infection rates in tsetse flies are low, rarely exceeding 0.1%, even in endemic areas.

8.3.1 Gambian sleeping sickness

Gambian sleeping sickness (*T. brucei gambiense*) is a form of the disease that occurs from West Africa through Central Africa to parts of Sudan and southwards to Angola and the Democratic Republic of the Congo. *Glossina palpalis* and *G. tachinoides* are the most important vectors in West Africa, while *G. fuscipes* is the vector in Central and East Africa. This disease is relatively chronic, with death often not occurring until after many years. Until recently it was considered that there were no natural animal reservoir hosts. Natural infections in pigs have been found in countries such as Cameroon and Equatorial Guinea, but whether they play any role as reservoir hosts is unclear.

Vectors of Gambian sleeping sickness are especially common at watering places, fords across rivers and along lake shores, etc., situations that people frequently visit to collect water or do their washing. As a consequence there may be limited and localized foci of transmission.

8.3.2 Rhodesian sleeping sickness

The causative agent of Rhodesian sleeping sickness, *T. brucei rhodesiense*, causes a more virulent disease than *T. brucei gambiense*, with death occurring

after just weeks or months. However, it is not so widespread, being more or less restricted to Tanzania, Malawi, Zambia, Zimbabwe, Mozambique and the northern areas of Lake Victoria in Kenya and Uganda. The most important vectors are *G. morsitans* and *G. pallidipes*, species which feed on a variety of game animals and domestic livestock, especially bovids, in preference to people. These flies often occur in savanna areas thinly populated by humans. Wild animals, especially various bovid species, are important reservoir hosts of *T. brucei rhodesiense*. Around Lake Victoria, *G. fuscipes* is the main vector and cattle are important reservoir hosts. This form of sleeping sickness is a ***zoonosis***.

8.4 Control

Because the larva is retained by the female for almost all of its life, and the puparium is buried in the soil, control of tsetse flies is aimed at the adults.

Many control methods have been directed at tsetse flies to combat human and animal trypanosomiasis. Formerly in Zimbabwe and some East African countries game animals in selected areas that might provide food for tsetse flies, or be reservoir hosts of trypanosomiasis, were killed. Such slaughter of animals is no longer acceptable in a world that is increasingly sensitive to the conservation of wildlife. Somewhat similarly, vegetation on which tsetse flies were known to rest was cut down, but again this ecologically destructive procedure is now rarely undertaken.

8.4.1 Insecticidal control

There are no problems with insecticide resistance in tsetse flies. Consequently pyrethroid insecticides such as permethrin, deltamethrin, lambda-cyhalothrin and cypermethrin can be sprayed onto vegetation harbouring adult flies. Success depends on a detailed knowledge of the resting sites of the vectors. For example, it is often possible to restrict spraying of tree trunks up to a height of 1.5 m during the dry season, extending this to 3.5 m in the wet season. Spraying is often done in the dry season so that deposits are not washed from vegetation by rainfall, and applications can remain effective for at least 2–3 months. However, extensive ground spraying is presently not widely used, because of concerns about the ecological contamination this can cause, but also because repeated spraying can be expensive.

Alternatively, ultra-low-volume (ULV) aerial insecticidal spraying can be undertaken. But because the droplets are too small to produce a persistent deposit on vegetation, and because the tsetse population is in the soil as puparia for 4–5 weeks, repeated sprayings are required, for example five or six times at 12- to 18-day intervals.

Although indiscriminate and repeated spraying of residual insecticides can have disastrous effects on the local fauna, it should be appreciated that application rates of insecticides for tsetse fly control are often very low (e.g.

20 mg active ingredient of deltamethrin per hectare). Furthermore, after flies have been controlled and spraying has stopped, many, if not all, of the wildlife may revert to their original population numbers. Intensive bush clearance for tsetse fly control can also greatly diminish the numbers and variety of the local fauna, but in this instance the change may be permanent, especially if people occupy and farm areas that were originally scrub or forest.

8.4.2 Targets and traps

Targets, sometimes called screens, made of dark blue or black cloth impregnated with pyrethroids (e.g. deltamethrin, lambda-cyhalothrin or cypermethrin) mounted on poles or hung from trees will kill tsetse flies attracted to these targets. Re-impregnation is needed every 3–4 months. Also biconical or pyramidal traps, incorporating dark blue or black cloth as an attractant, sometimes incorporating pyrethroids to kill flies resting on the outside of the traps, have been widely used to capture and kill tsetse flies. However, the care of such targets and traps is usually undertaken by local communities, and in many situations sustainability cannot be maintained. Most governments also lack the funding needed to maintain traps and targets.

8.4.3 Genetic control

Although genetic control, mainly using sterile male release methods (see Chapter 1, page 25), has sometimes been successful against tsetse fly vectors of cattle trypanosomiasis, even leading to the eradication of flies from Zanzibar, the approach is not generally feasible for sustained control of human sleeping sickness. An exception might be the use of genetic methods to eradicate residual populations of flies left locally after cheaper control methods (e.g. insecticides) have drastically reduced their numbers but failed to achieve eradication (see Simo *et al*. 2008).

8.4.4 Future control

The future of trypanosomiasis control will probably be based on insecticidal spraying and, where appropriate, drug therapy – for example, a combination of nifurtimox and eflornithine to treat Gambian sleeping sickness caused by *T. brucei gambiensis*.

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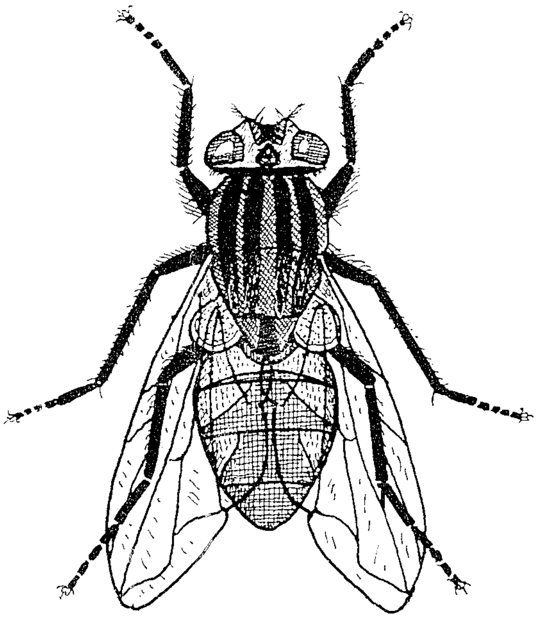
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9

House flies and stable flies (Muscidae) and latrine flies (Fanniidae)



There are some 18 000 species of true flies (sometimes called calyptrate Diptera), including medically important species in the families Glossinidae (Chapter 8), and the Muscidae and Fanniidae, which are described in this chapter.

The Muscidae contains about 4200 species of flies in 190 genera. The medically most important are the common house fly (*Musca domestica*), the greater house fly (*Muscina stabulans*) and the stable fly (*Stomoxys calcitrans*), all having a more or less worldwide distribution. House flies can be vectors of helminths, faecal bacteria, protozoans and viruses, resulting in the spread of enteric diseases (e.g. dysenteries and typhoids). The stable fly is a biting pest.

The family Fanniidae comprises about 280 species in four genera, but only species in the genus *Fannia*, such as *F. canicularis* (lesser house fly) and *F. scalaris* (latrine fly), are of medical importance, and like house flies they can transmit various pathogens to humans.

9.1 The common house fly (*Musca domestica*)

9.1.1 External morphology

There are about 70 species of flies in the genus *Musca*. The most common is *M. domestica*, the house fly, which is almost worldwide but is least common in Africa, where it is largely replaced by two subspecies (*M. domestica curviforceps* and *M. domestica calleva*). Other important species are (1) the bazaar fly (*Musca sorbens*), which can be a great nuisance in Africa, Asia and the Pacific, (2) the notoriously troublesome bush fly (*M. vetustissima*) of Australia and (3) the face fly (*M. autumnalis*), which is a pest in both the Old and New Worlds. The appearance and biology of these *Musca* species are very similar. The morphology and biology of the house fly (*M. domestica*) are described here.

House flies are medium-sized ***non-metallic*** flies about 6–9 mm long, varying in colour from light to dark grey with some darker markings. They have four rather broad black longitudinal stripes on the dorsal surface of the thorax (Fig. 9.1a, Plate 11). The antennae, which are not easily seen, are concealed in depressions on the front of the face. Each antenna consists of three segments, the distal and largest of which is cylindrical and has a prominent hair, called an ***arista***, which has hairs on ***both*** sides.

The mouthparts (proboscis) are specially adapted for sucking up fluid or semifluid foods. When not in use they are partially withdrawn into the head capsule (Fig. 9.2a), but are extended downwards in a telescopic fashion when the fly feeds (Fig. 9.2b). The proboscis ends in a pair of oval-shaped fleshy ***labella***, having very fine channels called ***pseudotracheae*** through which fluids are sucked up. House flies feed on many types of substances, including almost all food of humans, rotting vegetables,

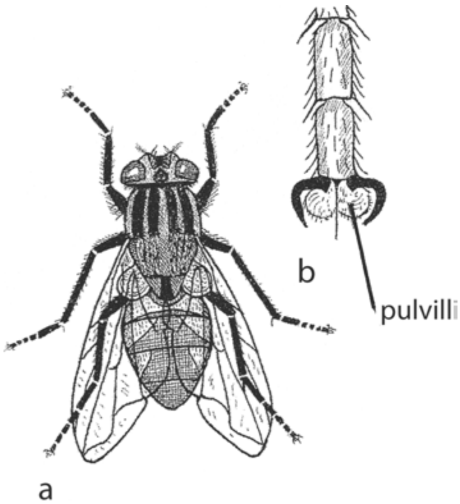


Figure 9.1 House fly (*Musca domestica*): (a) adult fly; (b) terminal tarsal segments, showing paired claws, paired large pulvilli and a single central bristle-like empodium.

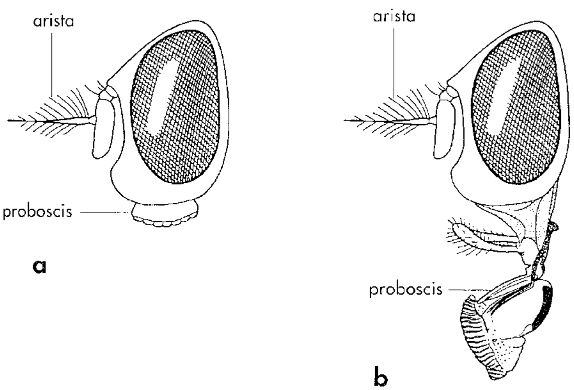


Figure 9.2 House fly (*Musca domestica*): (a) lateral view of head of adult with proboscis retracted; (b) proboscis extended for feeding.

carcasses, excreta and vomit – in fact almost any organic material. The method of feeding differs according to the physical state of the food. For example, for thin fluids, such as milk and beer, the labella are placed in contact with food, which is then sucked up through small openings in the pseudotracheae. When feeding on semisolids such as excreta, sputum and nasal discharges, the labella are completely everted and food is sucked up directly into the food channel. When flies feed on more solid materials such as sugar lumps, dried blood, cheese and cooked meats, the labella are

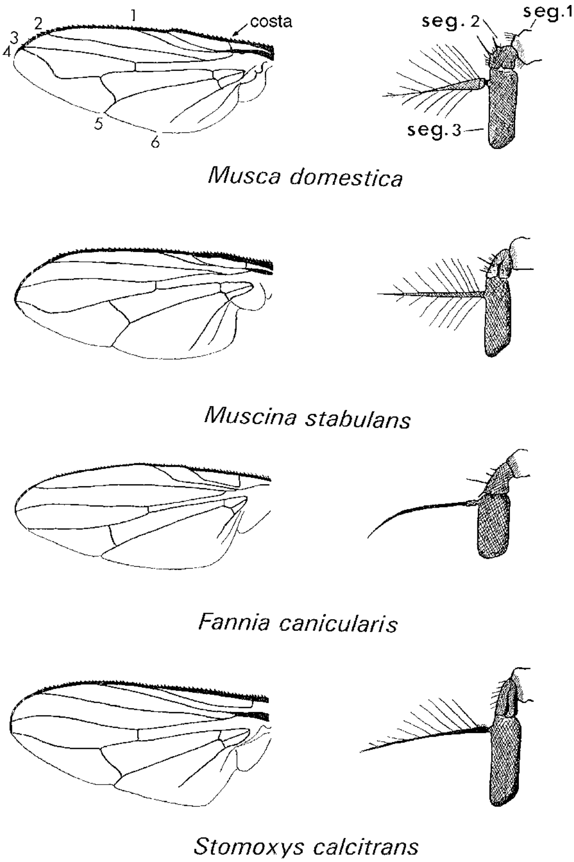


Figure 9.3 Wing venation and antennae characteristic of the genera *Musca*, *Muscina*, *Fannia* and *Stomoxys*. Note endings of veins 3 and 4.

everted and minute prestomal teeth surrounding the food channel are exposed and scrape the solid food. The fly then moistens small food particles with either saliva or the regurgitated contents of its crop so that food can be sucked up. This latter type of feeding is clearly conducive to the spread of a variety of pathogens.

The wings of the house fly have ***vein 4*** bending up sharply to join the costa (a thick vein along the front edge of the wing) close to vein 3 (Fig. 9.3). This is an important identification character which helps distinguish *Musca* species from other rather similar flies. All three pairs of legs end in paired claws and a pair of fleshy pad-like structures called the ***pulvilli***, which are supplied with glandular hairs (Fig. 9.1b). These sticky hairs enable the fly to adhere to very smooth surfaces, such as windows. They are also responsible for the fly picking up pathogens when it visits excreta, septic wounds,

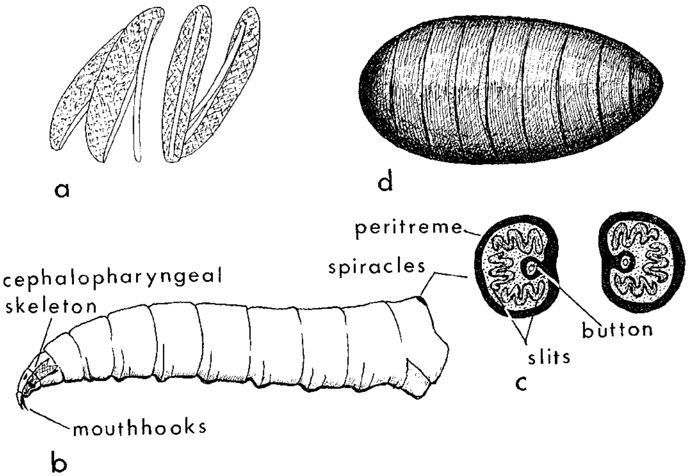


Figure 9.4 House fly (*Musca domestica*): (a) two hatched and two unhatched eggs; (b) final-instar larva; (c) posterior larval spiracles, showing their D-shape; (d) puparium.

rubbish dumps, etc. There are four visible greyish abdominal segments, which are usually partially obscured by the wings.

9.1.2 Life cycle

Female *Musca domestica* lay their eggs on decomposing materials such as animal manure, poultry dung, urine-contaminated bedding, carcasses, decomposing organic materials found in rubbish dumps, household garbage and waste foods from kitchens. Some 75–150 eggs are deposited together, or in separate batches. A fly may lay eggs 5–10 times in her lifetime, sometimes totalling up to 1000 eggs. The eggs are creamy-white, 1–1.2 mm long, and distinctly concave dorsally, giving them a banana-shaped appearance (Fig. 9.4a). They can hatch after only 10–16 hours, but this period is longer in cool weather. Hatching is accomplished by the strip of eggshell between parallel ridges on the dorsal concave surface lifting up, and partially detaching itself from the rest of the egg. Eggs cannot withstand desiccation and die if they dry out. Neither can they tolerate extremes of temperatures, most dying after exposure to temperatures below 15 °C or above 40 °C.

Larvae, known as ***maggots***, have a small head followed by an 11-segmented cylindrical body (Fig. 9.4b). At the pointed head end a pair of blackish small curved mouthhooks can be seen beneath the integument, and these are continued as the cephalopharyngeal skeleton in the anterior thoracic segments. At the posterior end of the body there is a pair of

conspicuous ***spiracles*** shaped like a ***letter D***. Each spiracle has a complete and thick outer wall called the ***peritreme***, which encloses three very sinuous spiracular slits (Fig. 9.4c).

Larvae feed on liquids from decomposing organic material. There are three larval instars. Mature larvae measure about 8–14 mm, the final size depending on environmental conditions, especially the amount of available food. The speed of larval development depends on the abundance of food and temperature. It may be completed in just 3–5 days, but under less favourable conditions 7–10 days are needed, and in cool weather development may extend to about 24 days.

Prior to pupation third-instar larvae often move to drier ground. Sometimes, however, the periphery of breeding places, such as rubbish dumps, may be sufficiently dry for larvae to pupate there; pupation may also occur in dry soil under larval habitats. Pupation begins with the larval skin contracting, hardening and turning dark brown, resulting in a barrel-shaped structure about 6 mm long, called a ***puparium***. Closer examination reveals that the puparium is segmented (Fig. 9.4d). The puparium is commonly called the pupa, but technically this is incorrect because the actual pupa is formed within the protective shell of the puparial case. A puparium is also formed by tsetse flies (Chapter 8) and by myiasis-causing flies (Chapter 10). The puparial stage lasts about 3–5 days in warm weather but 7–14 days during cooler periods.

Developmental time from egg to adult (Fig. 9.5) is about 49 days at 16 °C, 25 days at 20 °C, 16 days at 25 °C, 10–12 days at 30 °C and 6–7 days at 33 °C. Very occasionally at higher temperatures the period can be less than 7 days. Immature development ceases at temperatures below 12 °C, and 45 °C is lethal to the eggs, larvae and puparia. In temperate areas a varying, but usually small, proportion of house flies survive through the winter as puparia, but more frequently they overwinter as hibernating adults.

The adult fly escapes from its puparial case by pushing off its anterior end and crawling out, and after a short period it flies away.

Adult *Musca domestica* generally avoid direct sunlight, preferring to shelter in buildings inhabited by people or their animals. House flies and related flies, as well as the calliphorid flies (Chapter 10), are often called domestic or ***synanthropic*** flies, because of their close association with humans and their homes. House flies defecate at random, and frequently regurgitate their food, resulting in unsightly 'fly spots'. Adults tend to stay within 500 m of their breeding sites, but may fly 1–5 km or sometimes even further.

The bazaar fly (*Musca sorbens*) is widely distributed in Africa and parts of Asia, where it is a greater pest than *M. domestica* because adults more commonly settle around the eyes, on sweaty skin, suppurating wounds, and other body secretions than does the common house fly.

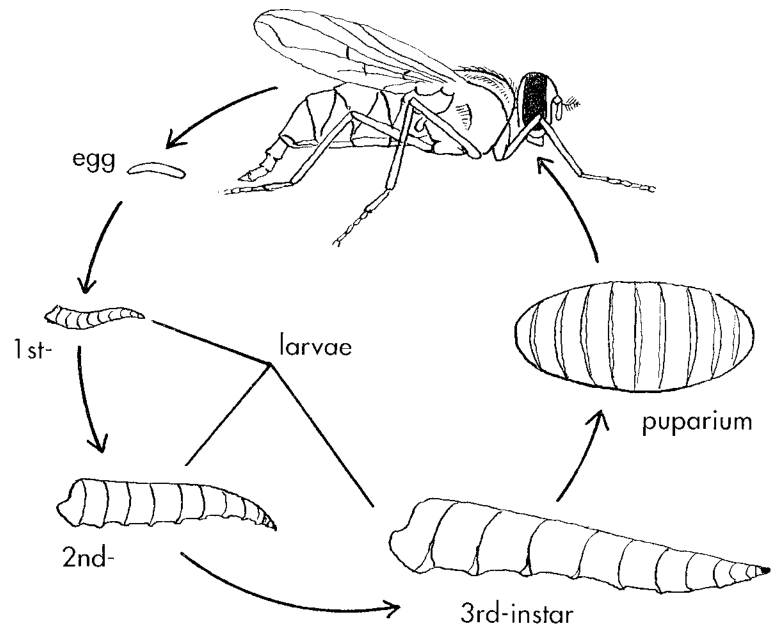


Figure 9.5 Life cycle of the house fly (*Musca domestica*), which is also typical of other muscid and calliphorid flies (Chapter 10).

9.1.3 Medical importance

House flies can transmit a large number of infections to humans because of their habits of visiting, almost indiscriminately, faeces and other unhygienic matter and people's food. Pathogens can be transmitted by three possible routes:

(1) By flies' contaminated feet, body hairs and mouthparts. Most pathogens, though, remain viable on the fly for less than 24 hours, and there are usually insufficient numbers to cause a direct infection, except possibly with *Shigella*. However, if pathogens are first transferred to food they may then multiply sufficiently to reach the level of an infective dose.
(2) By flies vomiting on food during feeding, which they do frequently.
(3) By defecation, which often occurs on food. This is probably the most important method of transmission.

It appears that more than 100 different pathogens have been recorded from house flies, and that at least 65 of them can be transmitted to people. With the exception of *Thelazia* species (eye-worms) transmission is mechanical, that is the fly acts just as a physical carrier.

House flies can transmit ***viruses*** of polio, Coxsackie and infectious hepatitis; ***rickettsiae*** of Q fever (*Coxiella burnetii*); ***bacteria*** such as anthrax, *Campylobacter*, cholera (*Vibrio cholerae*), *Shigella* and *Salmonella*, *Escherichia coli*, *Staphylococcus aureus*; ***spirochaetes*** of yaws (*Treponema pertenue*); ***protozoans*** including *Entamoeba*, *Cryptosporidium* and *Giardia*. In addition, house flies can carry eggs of a variety of helminths, for example *Taenia*, *Ancyostoma*, *Dipylidium*, *Diphyllobothrium*, *Enterobius*, *Trichuris* and *Ascaris*. Eye-worms (*Thelazia* species) are rather rare infections of the eye and are transmitted biologically by *Musca* species. Fungal infections such as *Microsporum canis*, causing 'tinea capitis' in humans, have also been found in fly excreta.

It seems that because house flies do not commonly rest on or near the eyes they are unlikely to be important vectors of trachoma (*Chlamydia trachomatis*). In marked contrast, adults of the bazaar fly (*Musca sorbens*) frequently settle on or around the eyes and have been shown to play an important role in the transmission of trachoma. Consequently in trachoma-endemic areas their breeding sites, such as human faeces, should be eradicated or at least greatly reduced.

In the tropical Americas house flies can also carry the eggs of *Dermatobia hominis*, a myiasis-producing fly (Chapter 10).

Larvae of house flies have occasionally been recorded causing urogenital and traumatic myiasis, and more rarely aural and nasopharyngeal myiasis. If food infected with fly maggots is eaten, then they may be passed more or less intact in the excreta, often causing considerable alarm and surprise. There is, however, no true intestinal myiasis in humans (see Chapter 10 for accounts of myiasis).

Although house flies are potential vectors of many pathogens to humans, it may be difficult to assess their importance in disease transmission because their role in the spread of disease is often circumstantial – for example, seasonal increase of fly abundance associated with outbreaks of diarrhoeal diseases.

A classic demonstration of the association between flies and disease was in two groups of Texan towns in 1946 and 1947. One group was sprayed with DDT to destroy house flies, and this was accompanied by a reduction in acute diarrhoeal diseases and deaths in children due to *Shigella*, although *Salmonella* infections remained the same. The unsprayed town did not have any reduction in *Shigella* infections. Later the unsprayed towns were sprayed and the towns previously sprayed left unsprayed. The incidence of dysentery in the two groups was now reversed. In 1988 control of house flies by attractant traps in an Israeli army camp resulted in a reduction in *Shigella* infections and also apparently enterotoxigenic *Escherichia coli* (ETEC) infections. More recently, in 1995 and 1996, when breeding sites in Pakistani villages were sprayed with insecticides fly populations decreased by about 97%

and the incidence of childhood diarrhoea decreased by 23%. Similarly in the Gambia, ultra-low-volume (ULV) spraying with deltamethrin in 1997 and 1998 reduced fly populations by about 75% and there were 75% fewer new cases of trachoma; diarrhoea in children was reduced by 25%. There is now considerable evidence that house flies can contribute to ill health.

In 2004 investigations in a Misrata city hospital in Libya demonstrated that house flies were carrying antibiotic-resistant bacteria, including methicillin-resistant *Staphylococcus aureus* (MRSA).

9.1.4 Control

Control methods can be divided conveniently into three categories:

(1) physical and mechanical control
(2) environmental sanitation
(3) insecticidal control

Physical and mechanical control

Flies can sometimes be prevented from entering buildings by covering doors and openings with plastic screening having a mesh size of 3–4 strands per centimetre (i.e. 2–3 openings per cm). Screening can be costly, but may be worthwhile in hospitals and restaurants. Although screening can reduce fly nuisance, flies will continue to breed locally and enter unscreened houses.

Air currents, such as the air barriers found in the entrances of some shops, and fans mounted over doorways, may reduce the number of flies entering premises. Placing curtains of vertical, often coloured, strips of plastic or beading in doorways also helps to keep out flies. Restaurants, food stores and hospitals often mount ultraviolet light-traps on walls to attract flies, which are then killed by an electric grid. Commercially available sticky tapes ('fly-papers'), incorporating sugar as an attractant, can be relatively effective, although unsightly, in catching flies.

Environmental sanitation

This aims at reducing house fly populations by minimizing their larval habitats, that is ***source reduction***. For example, domestic refuse and garbage should be placed either in strong plastic bags with the openings tightly closed, or in dustbins with tight-fitting lids. When possible there should also be regular refuse collections, preferably twice a week in warm countries, to prevent eggs laid in the garbage developing into adults. If household refuse cannot be collected it should be burnt or buried. Unhygienic rubbish dumps, often found in towns and villages, provide

ideal breeding places for house flies, and should be removed. Instead refuse should be placed in pits and covered, daily if possible, with a 15 cm layer of earth; when the pits are more or less full they must be covered with 60 cm of compacted earth. This depth of final fill is required to prevent rodents burrowing into the rubbish pits.

Insecticidal control

Insecticide resistance develops very quickly in house flies. Worldwide they have become resistant to the organophosphates, pyrethroids and carbamates. Although resistance to insect growth regulators (IGRs) is not presently a problem it has nevertheless been reported in some situations, such as in southwestern Turkey. In the absence of known resistance, insecticides such as bendiocarb (carbamate), malathion (organophosphate) and pyrethroids such as permethrin and cypermethrin can be used. However, the risk of developing resistance is increased if the same compound is used on the adult flies and their larval habitats. Also, the speed of becoming resistant is greater with residual sprays than with other treatments aimed at adult flies. The WHO warns against the intensive use of pyrethroids for residual spraying.

Larvicides Insecticides can be directed against the larvae by spraying the insides of dustbins, as well as refuse and garbage heaps, manure piles and other breeding sites. IGRs such as diflubenzuron, cryomazine or pyriproxyfen are also used. Usually large volumes (0.5–5 litres/m^2) are needed to penetrate the upper 10–15 cm of breeding sites to reach the larvae.

Spraying against adults Commercial aerosol spray cans or small hand sprayers can be used indoors to kill adult flies. Suitable insecticides include organophosphates such as malathion or pyrethroids such as permethrin. There must be care not to contaminate food with insecticides. Aerosol applications and space-spraying have virtually no residual effects: consequently treatments have to be repeated, and this can be costly. Furthermore, this approach does little to alleviate the source of the fly nuisance.

Outdoor aerosol applications or aerial ULV spraying with pyrethroids can give effective control in and around dairies, farms, markets and recreational areas. Usually, however, only temporary relief from flies is achieved, because outdoor spraying does not usually kill indoor-resting flies, prevent their reinvasion from outside the treated area, or prevent the emergence of new flies from breeding places.

Residual spraying Flies may also be controlled by spraying indoor walls, ceilings, doors, etc. with residual insecticides such as the organophosphates

or the carbamate bendiocarb. (According to the WHO, pyrethroids are best avoided so as to minimize pyrethroid resistance: see above.) Residual insecticides should remain effective for 1–2 months, but this depends on local conditions. Outside walls of houses and cattle sheds can also be sprayed with residual insecticides, but in dairies carbamates should be avoided. The duration of insecticidal effectiveness varies from a few weeks to a few months.

The outsides of dustbins and adjacent walls should also be sprayed to deter gravid (egg-laden) flies from ovipositing in dustbins and other nearby breeding places.

Insecticidal cords Cords or rope strips soaked in insecticides, but preferably not carbamates for health reasons, and dyed, preferably red, to alert people that they are impregnated with insecticides, can be hung up in dairies and other premises. They remain effective in killing flies resting on them for 2–6 months, depending on the insecticide and the dosage.

Toxic baits Dry baits consist of sugar mixed with bran or crushed corncobs, or some other inert carrier treated with insecticides. They provide an attractive but lethal solid bait which can be scattered on floors or placed in trays; they need to be replaced about every two days. Liquid baits commonly comprise 10% sugar solution and an insecticide. This is placed in a glass bottle inverted over a saucer-like receptacle so that as the bait evaporates more flows in from a reservoir, as in automatic feeders for poultry. The most commonly used insecticides in both dry and liquid baits include propoxur and diazinon. Newer insecticidal compounds are spinosad (a biopesticide originating from soil bacteria) and imidacloprid and thiamethoxam (both neonicotinoid pesticides that recently have devastated honey bee populations when used against agricultural pests). Commercially prepared dry or liquid baits are also sometimes available. The house fly sex pheromone muscalure can be added to baits to make them more attractive.

Viscous paint-on baits comprising an insecticide, sugar and a binder can be painted on a variety of vertical or horizontal surfaces and remain effective for 1–2 months, or longer. Baits can sometimes quickly reduce fly populations.

9.2 The greater house fly (*Muscina stabulans*)

9.2.1 External morphology

Muscina stabulans has a worldwide distribution and is commonly called the greater house fly, or false stable fly. Adults are about 7–10 mm long, slightly

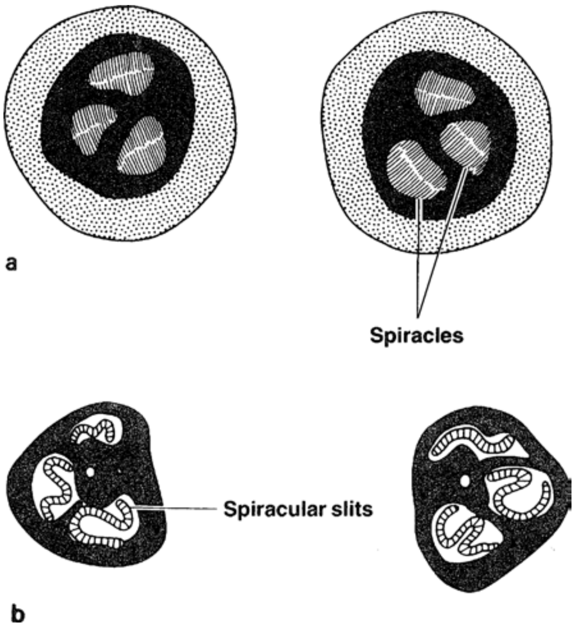


Figure 9.6 Pairs of posterior larval spiracles: (a) greater house fly (*Muscina stabulans*); (b) stable fly (*Stomoxys calcitrans*).

larger than house flies. They are distinguished from both *Musca* and *Fannia* species because ***vein 4*** of the wing curves slightly, but distinctly, upwards towards vein 3 (Fig. 9.3), and from *Fannia*, but not *Musca*, by having hairs on ***both*** the upper and lower sides of the arista (Fig. 9.3).

9.2.2 Life cycle

Females scatter their eggs mainly on decaying organic matter and human and animal excreta. Eggs hatch after 1–2 days and the resultant larvae resemble the maggot-shaped larvae of the house fly, but can be distinguished by having almost ***circular*** posterior ***spiracles***, not D-shaped as in *M. domestica*. Furthermore, the ***peritreme***, which is very wide, encircles three ***crescent-shaped*** spiracular slits (Fig. 9.6a). Young larvae are omnivorous scavengers, but towards the end of the larval period they become predaceous, feeding on other fly larvae. The brown puparium is similar to that of *M. domestica* and its duration is about 1–2 weeks. The life cycle lasts about 4–6 weeks, although in warm weather it may be reduced to 20–25 days.

Adults feed and behave much like adults of *M. domestica*, and may enter buildings.

9.2.3 Medical importance

Adults frequently defecate on food, but the exact role of *M. stabulans* as a disease vector remains undetermined. However, many of the pathogens transmitted by the house fly are probably also spread by this species. Larvae, like those of *Fannia* and *Musca*, are occasionally found in stools, but there is no true intestinal myiasis.

9.2.4 Control

Control measures are very similar to those for the house fly.

9.3 The stable fly (*Stomoxys calcitrans*)

9.3.1 External morphology

Stable flies have a worldwide distribution. They are sometimes known as biting house flies or, in the USA as dog flies (because they commonly bite dogs). The most common species is *Stomoxys calcitrans*. Adults have four black longitudinal stripes on a dark grey thorax and are about the size (5–7 mm) of house flies, which they superficially resemble. They are, however, easily separated from *Musca, Fannia* and *Muscina* by their conspicuous forward-projecting, ***rigid proboscis*** (Fig. 9.7, Plate 12). Wing venation resembles that of *Muscina*, but the ***arista*** of the third antennal segment differs from both *Musca* and *Muscina* in having hairs ***only*** on the upper side (Fig. 9.3).

In Africa adults could be confused with tsetse flies, which also have a forward-projecting proboscis (Chapter 8), but *Stomoxys calcitrans* is a smaller fly. Also, when at rest the wings are kept apart as in house flies and not placed completely over the body in a closed scissor-like fashion, as in tsetse flies. Furthermore, unlike tsetse flies, there is no enclosed hatchet cell in the wings.

9.3.2 Life cycle

Both ***males and females*** take blood-meals from wild and domesticated animals, including cattle, horses, pigs and dogs; they also feed on humans, especially if their preferred hosts are absent or scarce. During feeding the forward-projecting proboscis is swung downwards and the skin penetrated; bites can be painful, and most are on the legs. In hot weather blood-meals are digested within 12–24 hours and adults feed about every 1–3 days, but in cooler conditions blood digestion takes 2–4 days or longer, and feeding occurs every 5–10 days. ***Biting*** is restricted to the daytime and occurs both in bright sunshine and in cloudy weather. Although most biting is outdoors, stable flies will also enter houses to

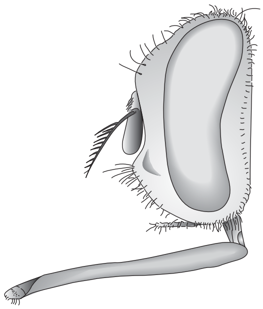


Figure 9.7 Lateral view of the head of stable fly (*Stomoxys calcitrans*), showing the forward-projecting proboscis.

feed. Adults are mostly encountered in and around farms or where horses are kept, and consequently they are more common in rural areas than in towns.

Their creamy-white eggs resemble those of house flies and are usually laid in batches of less than 20, but sometimes as many as 50–200 may be laid together, and 100–800 eggs may be laid in the fly's lifetime. Eggs are usually deposited in horse manure but also in compost pits, decaying and fermenting piles of vegetable matter, weeds, cut grass or hay. Stable flies very rarely lay their eggs in human or animal faeces, unless these are liberally mixed with hay or straw.

Eggs hatch within 1–5 days and the resultant larvae are creamy-coloured ***maggots*** which resemble those of the house fly. However, they can be separated by having the posterior ***spiracles*** widely separated (Fig. 9.6b), thus differing from those of *Musca* and *Muscina*. Spiracles are approximately round, lack a conspicuous ***peritreme***, and the S-shaped spiracular slits are widely separated from each other. Larvae prefer a high degree of moisture for development and are found mostly in wet mixtures of manure and soil or straw, and in vegetable matter in advanced stages of decay. Under optimum conditions the larval period lasts about 6–10 days, but in cooler weather, or when there is a shortage of food, development can be prolonged to 4–5 weeks or more.

Larvae migrate to drier areas and bury themselves in the soil prior to pupation. The puparium is dark brown and resembles that of the house fly, but can be distinguished from it by having the posterior spiracles widely separated. The puparial stage usually lasts 5–7 days, although in cool weather it may be extended to several weeks. The life cycle from egg-laying to adult emergence takes 12–13 days at 27 °C, but longer at cooler temperatures.

In tropical areas stable flies breed continuously throughout the year. In more temperate climates they pass the cooler months as larvae or puparia,

but sometimes adults survive the winter in warm stables or buildings, feeding intermittently during the cooler months.

9.3.3 Medical importance

Because of their painful bites ***both sexes*** of stable flies can be troublesome pests of people, cattle, horses and pets – notably dogs. Adult flies are not regarded as transmitting diseases to humans, and although they can be mechanical vectors of African trypanosomiasis there is little evidence that they play any part in the epidemiology of sleeping sickness. Because stable flies rarely visit excreta and festering wounds they are much less likely to spread pathogens in the way that house flies do.

In the tropical Americas eggs of *Dermatobia hominis*, a myiasis-producing fly (Chapter 10), are sometimes attached to adult stable flies.

9.3.4 Control

Many of the control methods aimed at house flies can be applied with some modification to control stable flies – for example, not allowing piles of manure, grass cuttings or decaying vegetable matter to accumulate, and burning waste straw and bedding material. Larval habitats can be sprayed with insecticides, but as noted with house fly control it is often difficult to get insecticides to penetrate deeply to where most larvae are found. Insecticidal spraying of horse stables, animal shelters, barns and other farm buildings can help reduce the numbers of stable flies.

9.4 The lesser or little house fly and the latrine fly (*Fannia* species)

9.4.1 External morphology

In this book I have placed the genus *Fannia* in the family Fanniidae, but some authorities place it in the family Muscidae.

Adult flies of *Fannia* resemble house flies but are a little smaller (5–7 mm). They are readily distinguished from house flies by having ***vein 4*** of the wing almost parallel to vein 3 (Fig. 9.3), whereas in *Musca* it bends upwards and almost touches vein 3 at the wing apex, and in *Muscina* vein 4 also bends upwards but not to such an extent. In *Fannia* species the ***arista*** arises from the third antennal segment and is ***completely*** devoid of hairs (Fig. 9.3), whereas in both *Musca* and *Muscina* there are hairs on both upper and lower sides. In most other respects adult flies are similar to house flies.

Two common species of *Fannia* are of minor medical importance. They are *Fannia canicularis* (the lesser, or little, house fly), which occurs worldwide and is commonly encountered in houses, and *Fannia scalaris* (the latrine fly) which has a Holarctic distribution and is uncommon in

houses. Adults of *Fannia canicularis* have ***three*** rather faint dark longitudinal stripes on the thorax, whereas *F. scalaris* has ***two*** such stripes.

9.4.2 Life cycle

Eggs of the lesser house fly (*F. canicularis*) resemble those of the house fly. They are deposited on food, but also on urine-soaked bedding of humans and animals, compost heaps, decaying piles of grass, human and animal excreta and in poultry litter. The latrine fly (*F. scalaris*) usually lays her eggs in faeces – hence its common name. Larvae of *Fannia* species prefer wetter larval habitats than those of house flies and are often found in semiliquid material, such as runny faeces.

Eggs hatch after 1–2 days. *Fannia* larvae are very different to the maggot-shaped larvae of *Musca* and are unlikely to be confused with the larvae of other medically important flies. They are rather flattened dorsoventrally and have many thin, but conspicuous and characteristic, lateral and dorsal fleshy processes arising from the body which bear small spiniform secondary processes. Figure 9.8 shows minor differences between larvae of *F. canicularis* and *F. scalaris*. Larval development takes about 7–12 days but may be prolonged if habitats start to dry out. The puparium is brown and is similar in shape to the larva, also having lateral and dorsal fleshy processes. After 7–10 days the adult fly emerges. The life cycle often lasts about one month, which is considerably longer than in *Musca domestica*, but may under favourable conditions be completed within 13–22 days. Although adult *Fannia* species, especially *F. canicularis*, often enter houses, they do not settle on people or on their food as much as house flies, but tend to hover around the head in an annoying manner.

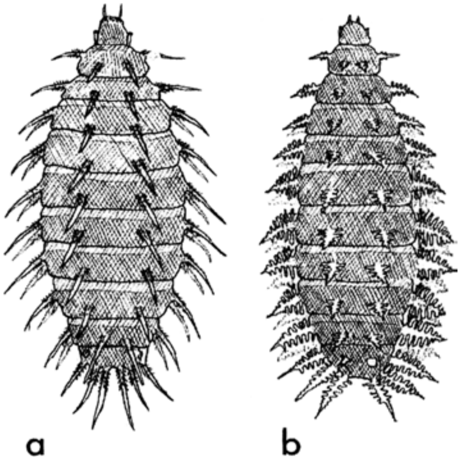


Figure 9.8 Final-instar larvae: (a) lesser house fly (*Fannia canicularis*); (b) latrine fly (*Fannia scalaris*).

9.4.3 Medical importance

Many of the pathogens transmitted by house flies are probably also spread by *Fannia* species. They have been incriminated in cases of aural and urogenital myiasis, and larvae are sometimes found in stools, but as previously stressed true intestinal myiasis does not occur in humans.

9.4.4 Control

The same control methods apply to species of *Fannia* as to *Musca*, but particular attention should be given to the prevention and eradication of *Fannia scalaris* breeding in latrines.

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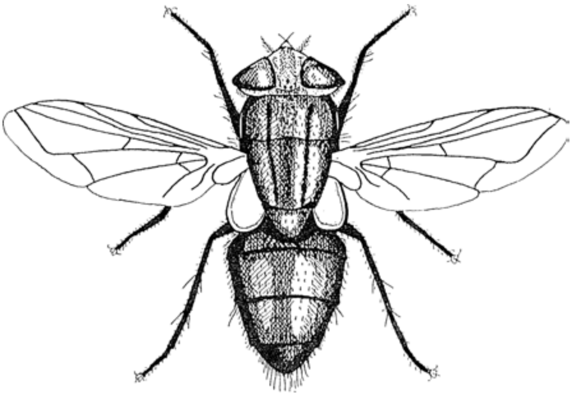
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10

Flies and myiasis



Myiasis is the invasion of organs and tissues of humans or other vertebrate animals by ***fly*** larvae, which at least for some time feed on the living or dead tissues or, in the case of intestinal myiasis, on the host's ingested food.

10.1 Types of myiasis

Myiasis may be accidental, obligatory or facultative.

Accidental myiasis usually involves eating food that is contaminated by eggs or larvae of flies that are not parasitic in mammals, such as house flies. Although the larvae may survive for some time in the intestine, no flies are specially adapted to cause intestinal myiasis in humans. (In contrast, obligatory intestinal myiasis occurs in other mammals.) The presence of larvae in the human intestine may nevertheless cause considerable discomfort, abdominal pain and diarrhoea, which may be accompanied by discharge of blood and vomiting. Living larvae may be passed in excreta or vomit.

In ***obligatory*** myiasis it is essential for the fly ***maggots*** (larvae) to live on a live host for at least a part of their life. For example, larvae of *Cordylobia anthropophaga*, *Cochliomyia hominivorax*, *Chrysomya bezziana*, *Dermatobia hominis* and *Wohlfahrtia magnifica* are all obligatory parasites of humans and other vertebrates.

In contrast, in ***facultative*** myiasis larvae are normally free-living, often attacking carcasses, but under certain conditions may infect living hosts. Several types of fly, including species of *Calliphora*, *Lucilia* (= *Phaenicia*), *Phormia* and *Sarcophaga*, which normally breed in meat or carrion, may sometimes cause facultative cutaneous myiasis in people by infecting festering sores and wounds. Occasionally facultative urogenital myiasis occurs in humans, usually involving larvae of *Musca* or *Fannia* species. Ovipositing flies attracted to unhygienic discharges lay their eggs near genital orifices, and on hatching the minute larvae enter the genital orifice and pass up the urogenital tract. Considerable pain may be caused by larvae obstructing these passages, and mucus, blood and eventually larvae may be discharged during urination.

Different terms are used to describe myiasis which affects different parts of the body – for example, ***cutaneous***, dermal or subdermal myiasis; ***urogenital*** myiasis; ***ophthalmic*** or ocular myiasis; ***nasopharyngeal*** myiasis; and ***intestinal***, gastrointestinal or enteric myiasis. When larvae burrow just under the surface layers of the skin this is sometimes called ***creeping eruption*** or creeping myiasis; when boil-like lesions are produced the term ***furuncular*** myiasis may be used; and when wounds become infested this is often referred to as ***traumatic*** myiasis.

When larvae occur in wounds, sores and dermal or subdermal tissues, their removal under aseptic conditions is usually relatively simple. When, however, they are more deeply imbedded in the underlying tissues, or

when they have penetrated the mucous membranes, eyes, frontal sinuses or cavities, their removal is more difficult and surgery may be needed. Major and irreversible damage may have been done by the larvae.

The biologies and medical importance of the principal types of flies causing facultative and obligatory myiasis in humans are outlined below.

10.2 Classification

Flies described in this chapter are in three families: the Calliphoridae, Sarcophagidae and Oestridae. The family Calliphoridae can be conveniently divided into two groups. One group contains the ***non-metallic*** flies such as the Congo floor-maggot fly (*Auchmeromyia senegalensis*) and the tumbu fly (*Cordylobia anthropophaga*), adults of both species being a dull brownish colour. The other group contains the ***metallic*** calliphorids, such as the blowflies, comprising the bluebottles (*Calliphora* species) and the greenbottles (*Lucilia* (= *Phaenicia*)), and the New World screwworms (*Cochliomyia hominivorax*) and Old World screwworms (*Chrysomya bezziana*). Adults of these flies are typically shiny green or bluish.

10.3 Calliphoridae: non-metallic flies

10.3.1 Cordylobia anthropophaga

Cordylobia anthropophaga, known as the tumbu or mango fly, is found in Africa from Ethiopia in the north through West and East Africa to Natal and the Transvaal in the south. There is little evidence that *C. anthropophaga* is found breeding outside Africa, although cases of infection have sometimes been reported.

External morphology

Adults are robust, relatively large flies, 9–12 mm long, dull yellowish to light brown but with two dark grey poorly defined dorsal longitudinal thoracic stripes (Fig. 10.1). There are four visible abdominal segments which are more or less ***equal*** in length (compare *Auchmeromyia senegalensis*, in which the second abdominal segment is markedly ***longer*** than the others). The wings are slightly brownish.

Life cycle

Females lay 100–300 eggs in several batches on dry soil or sand in shady places, especially those contaminated with the urine or excreta of humans, rodents, dogs or monkeys. Females also oviposit on underclothes or soiled babies' nappies (diapers) placed on the ground. The white banana-shaped eggs hatch after 1–3 days. Larvae attach themselves either directly to a

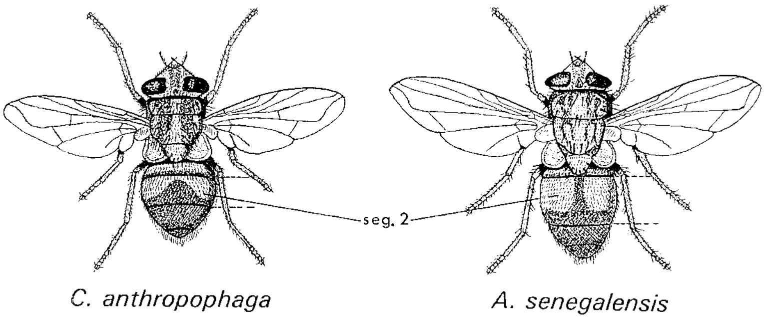


Figure 10.1 Adults of the tumbu fly (*Cordylobia anthropophaga*) and the Congo floor-maggot fly (*Auchmeromyia senegalensis*), showing the longer second abdominal segment in *A. senegalensis*.

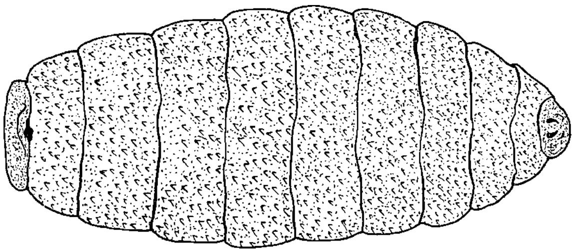


Figure 10.2 Final-instar larva of the tumbu fly (*Cordylobia anthropophaga*).

suitable host or to washed clothing placed on the ground to dry. Larvae get transferred to people if clothing is not ironed before it is worn. On a host a larva buries itself completely except for its posterior spiracles, situated at the tip of the abdomen, which remain in contact with the air. Newly hatched larvae can remain alive for 9–15 days on the ground in the absence of a suitable host.

Minute first-instar larvae are maggot-shaped (like the larvae of house flies), the second-instar larvae are club-shaped, and the third- and final-instar larvae are rather fat, broadly oval-shaped, yellowish-white and about 11–15 mm long. The larvae (maggots) are covered with numerous ***spicules***, which are often, but not always, grouped into three or more transverse rows per segment (Fig. 10.2, Plate 13). After 8–12 days mature larvae wriggle out of boil-like swellings and fall to the ground, where they bury themselves and turn into puparia. Adult flies emerge 8–15 days later and feed on rotting fruit, carrion and faeces. Adults readily enter houses, where they may lay their eggs on mud floors, especially if children have urinated on them.

Medical importance

Larvae of *Cordylobia* cause boil-like (furuncular) swellings on almost any part of the body. Although these swellings may become sore and inflamed, and even quite hard and exude serous fluids, they do not usually contain pus. Generally only one or two larvae are found in a patient; however, more than 60 larvae were recorded from one person, mostly in separate lesions. A larva can be removed by covering the hole in the swelling with medicinal liquid paraffin, which prevents it from breathing through its posterior spiracles. Consequently a larva wriggles a little further out of the swelling to protrude its spiracles, and this lubricates the pocket in the skin. The larva can then be extracted by gently pressing around the swelling.

Infections can be prevented, or at least minimized, by ensuring that clothes, bed linen and towels are not spread on the ground to dry, and also by ironing clothing.

Dogs and rats are commonly infected with tumbu larvae.

10.3.2 *Auchmeromyia senegalensis*

Auchmeromyia senegalensis, commonly known as the Congo floor-maggot fly, although not strictly speaking causing myiasis, is described here because adults are often confused with those of *Cordylobia anthropophaga*. The species occurs throughout most of Africa south of the Sahara and also in the Cape Verde Islands.

External morphology

Adults are very similar to *C. anthropophaga* but are distinguished by the second abdominal segment being about ***twice as long*** as any of the others (Fig. 10.1), whereas in the tumbu fly all segments are about equal in length.

Life cycle and medical importance

Some 300 eggs are laid in batches of about 50 on the dry sandy floors of mud huts. They hatch after 1–3 days and the larvae hide in cracks and crevices in the floor, especially under beds and sleeping-mats, or they burrow into the soil. At night they crawl out and take blood-meals from people sleeping on the floor, after which the now pinkish larvae return to their hiding places. Larvae may feed four or five times a week, but can withstand long periods of starvation in the absence of suitable hosts. There are three larval instars, each requiring at least two blood-meals. Under optimum conditions larval development is completed within 3–4 weeks, but it may be prolonged up to three months if larvae fail to obtain regular feeds. Third-instar larvae, unlike those of *Cordylobia anthropophaga*, are not covered with conspicuous spicules (Fig. 10.3). Because larvae cannot climb,

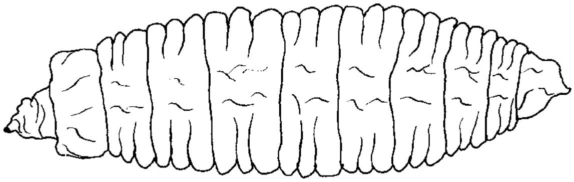


Figure 10.3 Final-instar larva of the Congo floor-maggot fly (*Auchmeromyia senegalensis*).

people will not be attacked if they sleep on beds raised from the floor. Mature larvae pupate in cracks or directly on the surface of mud floors. Adults emerge from the puparia after about 9–20 days and, like tumbu flies, feed on rotting fruit and faeces.

The Congo floor-maggot fly was formerly common in certain parts of Africa, but due to changes in lifestyle it is becoming increasingly rare, and these days is not much of a problem.

10.4 Calliphoridae: metallic flies

10.4.1 New World screwworms (*Cochliomyia*)

New World screwworms (*Cochliomyia hominivorax*) formerly occurred in the southern states of the USA, through Mexico, Central America, the Caribbean islands, into the northern parts of South America. However, following successful eradication programmes, achieved by the release of thousands of sterilized male flies, the screwworm has been eradicated from the USA, Mexico, the Virgin islands, Curaçao and Central America except for parts of Panama. Unfortunately programmes to eliminate the fly from Jamaica and Trinidad have failed.

In 1988 a population of the New World screwworm was discovered in Libya, but it was eradicated in 1991.

External morphology

Adult flies of *C. hominivorax* are 8–10 mm long, metallic green to bluish green, and have three distinct dark longitudinal stripes on the dorsal surface of the thorax (Fig. 10.4). ***Dorsal bristles*** on the thorax, like those of *Chrysomya*, are poorly developed, thus distinguishing screwworm flies from *Lucilia* (= *Phaenicia*) and *Calliphora*, which have well-developed bristles. The ***squama***, a membranous lobe on the posterior border of the wing near the thorax (Fig. 10.5a), is ***devoid*** of hairs, as in *Lucilia*.

Life cycle

Females lay batches of 10–200 eggs on the edges of wounds, scabs, sores or scratches, also on dried blood clots and on diseased or healthy mucous

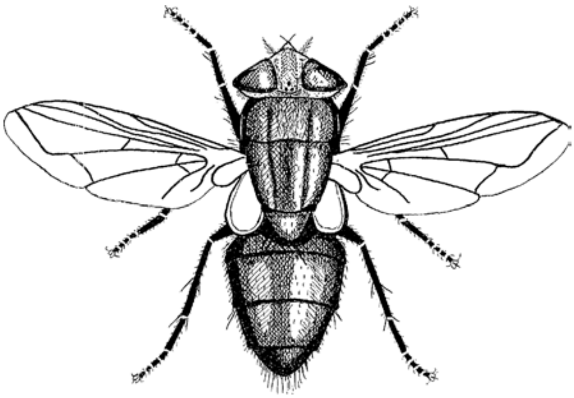


Figure 10.4 Adult of the New World screwworm fly (*Cochliomyia hominivorax*).

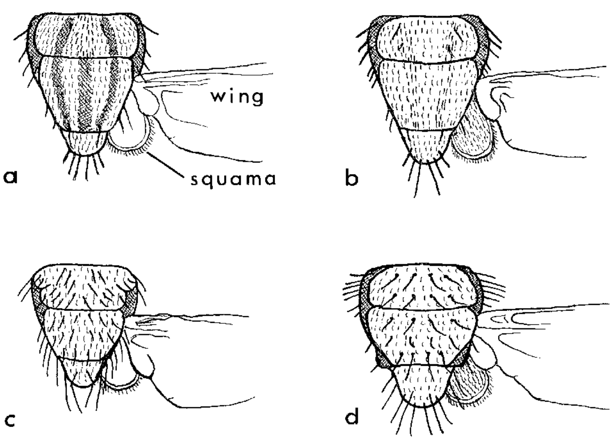


Figure 10.5 Thoraces of adult flies, showing the presence or absence of prominent dorsal bristles; and bases of the right wings, showing the presence or absence of fine hairs on the squama: (a) *Cochliomyia*: note the three dark thoracic stripes and squama lacking hairs; (b) *Chrysomya*: note the absence of prominent thoracic stripes and the hairy squama; (c) *Lucilia*: note the prominent thoracic bristles and squama lacking hairs; (d) *Calliphora*: note the prominent thoracic bristles and the hairy squama.

membranes such as the nasal passages, eyes, ears, mouth and vagina. In newborn babies eggs may be laid in the umbilicus. Eggs hatch after 10–24 hours and the active larvae burrow deeply into living tissues and feed gregariously. There are three larval instars, and the third-instar, which is formed after 2–4 days, is about 15–17 mm long and typically *maggot*-shaped. They are distinguished from house fly maggots by the presence of distinct ***bands of spicules*** encircling the anterior margins of all body

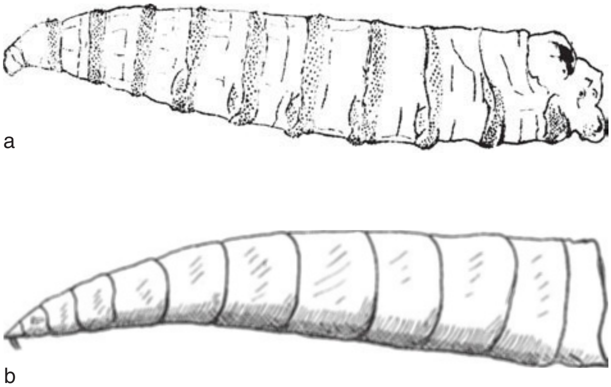


Figure 10.6 Final-instar larvae: (a) *Chrysomya* (*Cochliomyia* larvae are similar), showing bands of spicules on the segments; (b) *Lucilia* (*Calliphora* larvae are almost identical), lacking prominent spicules.

segments (Fig. 10.6a, Plate 14), and by the dark part of the tracheal trunks from the posterior spiracles extending into 3–4 abdominal segments. Larvae tend to penetrate deeply into tissues, so that infections near the eyes, nose and mouth can cause considerable destruction, often accompanied by putrid-smelling discharges and ulcerations.

After 4–12 days the larvae reach maturity and wriggle out of the wounds or passages they have excavated and drop to the ground, where they bury in the soil and pupate. In warm weather the puparial stage lasts about 7–10 days, but in cooler weather it may be prolonged for many weeks or even months. The life cycle from egg to adult is usually about 2–3 weeks.

10.4.2 Old World screwworms (*Chrysomya*)

The genus *Chrysomya* contains many species and is common in the tropics. About 10 species are known to cause myiasis in humans, but only *Chrysomya bezziana* is important because its larvae, like those of *Cochliomyia hominivorax*, are ***obligatory*** parasites of living tissues. *Chrysomya bezziana* occurs throughout tropical Africa, the Indian subcontinent, most of Southeast Asia to China, and the Philippines to Papua New Guinea. *Chrysomya bezziana* has also been introduced into several countries on the west coast of the Persian Gulf, including Iraq, Iran and Saudi Arabia. Larvae of other *Chrysomya* species are not obligatory parasites, and often develop in carrion and decomposing matter. However, ***facultative*** myiasis-producing species such as *Chrysomya albiceps* and *C. megacephala* of the Old World have invaded Central and South America.

External morphology

Adult *Chrysomya bezziana* are similar to *Cochliomyia hominivorax*, but they lack the distinctive longitudinal thoracic stripes, and the dorsal surface of the ***squama*** is covered with fine hairs (Fig. 10.5b). Larvae are very similar to those of *C. hominivorax*, but usually have 4–6 finger-like processes on the anterior spiracles, not the usual 7–9 found in *C. hominivorax*, and they can also be identified by the dark part of the tracheal trunks of the posterior spiracles, which extend into only one abdominal segment. In practice separation is usually easy: screwworms of the Americas belong to the genus *Cochliomyia* whereas those of the Old World belong to the genus *Chrysomya*.

Life cycle

The life cycle of *Chrysomya bezziana* is very similar to that of *Cochliomyia hominivorax*. About 150–200 eggs are deposited in wounds, open sores, scabs, ulcers, scratches or on mucous membranes, especially those contaminated with discharges. They hatch within 24 hours or less and newly emerged larvae burrow through the skin to the underlying tissues, where they commonly remain congregated together. Larvae complete their development in 5–7 days and then wriggle out of the wounds and drop to the ground, where they bury themselves and pupate. The puparial period lasts about 7–9 days in warm weather, but is prolonged to several weeks or even months during cold weather. The life cycle from egg to adult usually takes about 2–3 weeks.

Adults of both New and Old World screwworms frequently feed on decomposing corpses, decaying matter, excreta and flowers.

10.4.3 Medical importance of screwworms

Larvae of both *Chrysomya bezziana* and *Cochliomyia hominivorax* cause ***obligatory*** myiasis in humans, resulting in considerable damage and disfigurement, especially if the face is involved. When larvae invade natural orifices, such as the nose, mouth, eyes or vagina, they can cause excruciating pain and misery. In one patient suffering from a nasal infection 385 larvae of *C. hominivorax* were removed over a nine-day period! Larvae of both species may eat their way through the palate and as a result impair speech.

Chrysomya bezziana causes more cases of myiasis in people living in India and other parts of Asia than it does in Africa. *Chrysomya* adults often visit faeces, so are potential vectors of several pathogens.

Myiasis cases should be treated immediately, because the very rapid larval development can cause permanent damage. Maggots in open wounds or body openings can be removed by irrigating infested areas with ethanol or chloriform mixed with vegetable oil. More recently oral or topical use of ivermectin has resulted in killing the larvae. Surgery may be necessary to expose deeply embedded larvae. There are serious

problems with ocular myiasis, and delicate surgery may be needed to remove the larvae, but permanent damage may already have been done.

Both screwworm species, but particularly *C. hominivorax*, cause myiasis in cattle, goats, sheep and horses and cause enormous economic losses to the livestock industry. The technique of releasing millions of laboratory-reared sterile male flies into areas infested with screwworms has given good control, and has even resulted in the eradication of *C. hominivorax* from the USA, Mexico, most Central American countries, some Caribbean islands, as well as from Libya.

10.4.4 Greenbottles (*Lucilia* = *Phaenicia*)

Several species of greenbottles occur in the genus *Lucilia*, and although the genus has a worldwide distribution most species are in northern temperate regions. Some entomologists use the generic name *Phaenicia* instead of *Lucilia*.

External morphology

Adults are mostly metallic or coppery green (Plate 15), and are usually a little smaller (about 10 mm long) and a little less bristly than species of *Calliphora* (bluebottles). As in *Calliphora*, prominent ***bristles*** occur on the dorsal surface of the thorax, but the ***squama*** of the wing lacks hairs (Fig. 10.5c), whereas in bluebottles it is hairy dorsally. *Lucilia sericata* is the commonest species, occurring in the Americas, Europe, Asia, Africa, Australia and in most other areas of the world. Another common species, *L. cuprina*, occurs mainly in Africa, Asia and Australia.

Life cycle

Greenbottles usually lay their eggs on meat, fish, carrion and decomposing carcasses, but occasionally on or near festering and foul-smelling wounds of humans and animals, as well as on excreta and decaying vegetable matter. Eggs often hatch within 8–12 hours. Larvae are typically ***maggot***-shaped (Fig. 10.6b), and they may have very small spicules but not conspicuous ones like the larvae of screwworms, which they otherwise tend to resemble. They can also be distinguished from screwworms by the posterior spiracles having a complete ***peritreme***; in screwworms it is incomplete.

The larval period lasts about 5–8 days. Mature larvae bury in loose soil and pupate; the puparial period lasts about 6–15 days. The duration of the various life stages depends greatly on temperature and geographical area.

Adult flies frequently visit carrion, excreta, general refuse and decaying material, as well as sores and wounds. They are particularly common around unhygienic situations where meat or dead animals are present.

They are frequently abundant near slaughterhouses and piggeries. They commonly fly into houses, where they are particularly troublesome because of their noisy buzzing flight. The most common species infesting wounds of humans are *Lucilia sericata* and *L. cuprina*.

10.4.5 Bluebottles (*Calliphora*)

There are numerous species of flies, known as bluebottles, belonging to the genus *Calliphora*. Although *Calliphora* has a worldwide distribution, bluebottles are more common in the northern temperate regions than in the tropical or southern temperate regions. The most important species with regard to myiasis are *Calliphora vicinia* and *C. vomitoria*.

External morphology

Adults are robust flies, 8–14 mm long, dull metallic-bluish or bluish-black (Plate 16). As in *Lucilia*, there are well-developed ***bristles*** on the thorax, but the ***squama*** of the wing is hairy on the dorsal surface (Fig. 10.5d), whereas in *Lucilia* it lacks hairs. The abdomen is rather more shiny than the thorax.

Life cycle

Bluebottle larvae look very similar to those of *Lucilia*, and the life cycle is also very similar to that described for *Lucilia*.

10.4.6 Medical importance of greenbottles and bluebottles

The dirty habit of blowflies (greenbottles and bluebottles) of feeding on excreta, decaying material and virtually all foods makes them potential vectors of numerous pathogens. However, their medical importance is usually associated with ***facultative*** myiasis.

Larvae of both *Lucilia* and *Calliphora* often develop in foul-smelling wounds and ulcerations, especially those producing pus. In hospitals they may be found underneath bandages and dressings of patients, especially when these have become contaminated with blood and pus. Such infections do not usually cause any serious harm, since the larvae feed mainly on pus and dead tissues. In 1998 a patient in a hospital in the USA had about 100 larvae of *L. sericata* removed from nasal passages both manually and by nasal tracheal suction. Removal of maggots of *Lucilia* and *Calliphora* usually presents no problems, because they can be picked out of wounds with sterile forceps and antibiotic dressings applied. Only very rarely do maggots invade healthy tissues. Occasionally intestinal myiasis is reported. This is usually caused by eating food contaminated with larvae of *Lucilia* or *Calliphora*, but usually the larvae are killed within the human alimentary canal and no serious harm is done. As

previously emphasized (page 158), there is no obligatory intestinal myiasis in humans.

10.4.7 Maggot therapy

The Mayans of Central America, Australian aborigines and people in northern Myanmar have used maggot therapy for many centuries, and this practice continued in some parts of the world until about the 1950s. However, it seems that during the American Civil War (1861–5) the Confederate army surgeon J. F. Zacharias was the first Western physician to introduce maggots to clean wounds. Maggot therapy has been rediscovered, and doctors, particularly in the USA and the UK, but also other countries, mostly in Europe, are advocating the use of sterile larvae to clean up leg ulcers, pressure sores and infected surgical wounds. However, not all types of wound respond well to maggot therapy.

Several commercial companies breed colonies of the flies, the fly eggs produced are given an antiseptic bath, and the resulting first-instar larvae are then placed on a patient's wound. Fly maggots most frequently used are those of *Lucilia sericata*. Some patients need considerable persuasion to accept this unusual form of treatment! About 30 countries are now using maggot therapy, with about 60 centres in North America, 400 in the United Kingdom and more than 140 in Germany.

10.4.8 Control of greenbottles and bluebottles

The principal breeding places of greenbottles and bluebottles are domestic refuse, rubbish tips, dustbins, offal and other waste products from slaughterhouses and meat packing factories. Larvae are also found in foods such as meat and fish left out in the sun to dry. Any methods that reduce breeding sites should reduce local populations of adult flies. Dustbins and garbage cans should have tight-fitting lids and be emptied once or twice a week. The outsides of such bins and both sides of the lid should be sprayed with insecticides such as organophosphate or pyrethroids every 7–10 days, while adjacent walls and fences can be sprayed every two weeks.

Many of the insecticidal control measures used against house flies (Chapter 9) are applicable to controlling blowflies.

10.5 Sarcophagidae: flesh flies

Only species of *Sarcophaga* and *Wohlfahrtia* in the family Sarcophagidae are of medical importance. They are sometimes called flesh flies. They cause myiasis, and possibly act as mechanical vectors of pathogens. Females are

unusual because they are ***larviparous***, that is they deposit first-instar larvae instead of laying eggs. They have a worldwide distribution.

10.5.1 Sarcophaga

External morphology

Sarcophaga species are large and hairy ***non-metallic*** flies, about 10–25 mm long. They are usually greyish and have three prominent black longitudinal stripes on the thorax (Plate 17). The abdomen is sometimes distinctly, but other times indistinctly, marked with squarish dark patches on a grey background giving it a ***chequer-board*** (chess-board) appearance (Fig. 10.7).

Life cycle and medical importance

Adult *Sarcophaga* do not lay eggs but deposit first-instar larvae, as do tsetse flies and *Wohlfahrtia* species (i.e. they are ***larviparous***). Larvae are deposited in batches of 30–60, on decaying carcasses, human and animal excreta, rotting food, but occasionally in wounds. They are primarily scavengers. Larvae are ***maggot***-shaped. They are distinguished from larvae of the Calliphoridae by the ***posterior spiracles*** being situated in a deep pit (Fig. 10.8) and thus difficult to see, and also by having bands of ***spicules*** on the body. Larvae of *Sarcophaga* are virtually indistinguishable from those of *Wohlfahrtia* species.

Larval development in hot weather lasts only 3–4 days, after which the larvae bury in the soil and pupate. The puparial stage lasts about 7–12 days.

Although larvae are usually deposited in carrion they very occasionally occur in wounds and cause ***facultative*** myiasis, but usually causing little damage because they feed mainly on necrotic tissues. They have more commonly been incriminated in accidental intestinal myiasis, causing considerable discomfort and pain before the larvae are expelled in the faeces. The most common species is *Sarcophaga cruentata* (= *haemorrhoidalis*), which

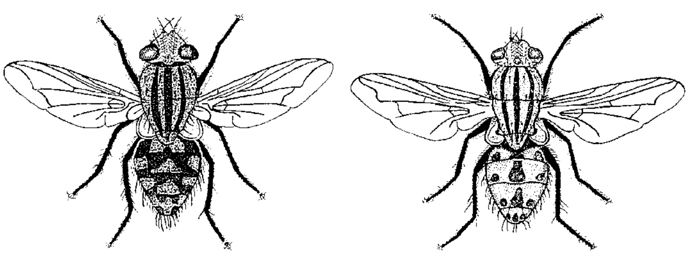


Figure 10.7 Adults of the flesh flies *Sarcophaga carnaria* and *Wohlfahrtia magnifica*, showing differences in their abdominal markings.

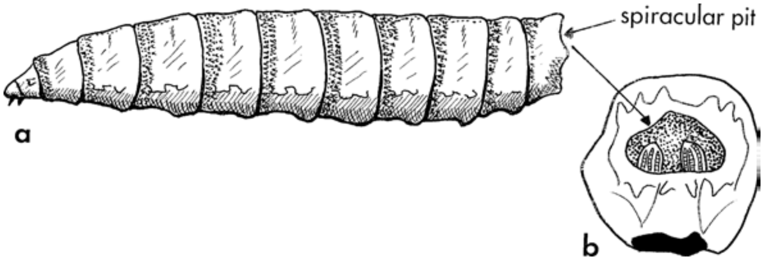


Figure 10.8 Larva of *Sarcophaga*, showing (a) bands of spicules on the segments and (b) the deep pit in which the posterior spiracles are located (*Wohlfahrtia* larvae are almost identical).

is widely distributed in the Americas, Europe, Africa and Asia, while *S. carnaria* is common in the Palaearctic region. Because adults frequent festering wounds, excreta and decaying animal matter they may be mechanical vectors of various pathogens.

10.5.2 Wohlfahrtia

External morphology

Wohlfahrtia species are hairy flies, 8–15 mm long, about as large as bluebottles or a little larger. They are greyish and like *Sarcophaga* have three distinct black lines on the thorax. The dark markings on the abdomen, however, are not in the form of a chess-board pattern as in *Sarcophaga* species, but are usually present as ***roundish*** lateral spots and triangular-shaped dark markings along the midline (Fig. 10.7). There is, however, considerable variation, and sometimes the dark marks are so large as to be more or less confluent, making the abdomen appear mainly black.

Life cycle and medical importance

As with *Sarcophaga* and tsetse flies, adults of *Wohlfahrtia* deposit ***larvae*** not eggs. The most important species in the Old World is *W. magnifica*, which causes ***obligatory*** myiasis in humans and animals (e.g. camels, domestic livestock and dogs) in western Europe, the Middle East, North Africa and Central Asia to China. A gravid female may deposit 120–170 larvae, often in several batches, in scratches, wounds, sores and ulcerations. In people the ears, eyes and nose are frequently infested, and this can cause deafness, blindness and even death. The New World species, *W. vigil* and *W. opaca*, will also deposit their larvae on unbroken skin if it is soft and tender, such as in babies and very young children, who are, therefore, more commonly attacked than adults. The maggots cause ***furuncular*** myiasis.

Wohlfahrtia larvae have bands of ***spicules***, and the ***spiracles*** are situated in a deep pit (Fig. 10.8), closely resembling larvae of *Sarcophaga*. Larval development takes 5–9 days, after which mature larvae drop to the ground, bury themselves in loose soil and pupate. Adults emerge from the puparia after 8–12 days.

Like the larvae of screwworms, *Wohlfahrtia* larvae can burrow deeply into the tissues and cause considerable damage.

10.6 Oestridae: bot flies

The family Oestridae comprises four subfamilies, one of which, the Cuterebrinae, contains 58 species in two genera that cause myiasis in rodents, monkeys and livestock, and the bot fly (*Dermatobia hominis*). This fly causes ***obligatory*** myiasis in people and animals, mainly cattle, living in southern Mexico to Argentina and Chile.

10.6.1 Dermatobia hominis

External morphology

Adult *Dermatobia hominis* are a little larger (12–18 mm) than bluebottles (*Calliphora*), with a similar dark-blue ***metallic-coloured*** abdomen and dark bluish-grey thorax, but the head is mainly yellowish (Fig. 10.9). The mouthparts are vestigial. Although they are primarily pests of cattle, *D. hominis* also infest humans, hence their name human bot fly. They are also sometimes called tórsalo or berne.

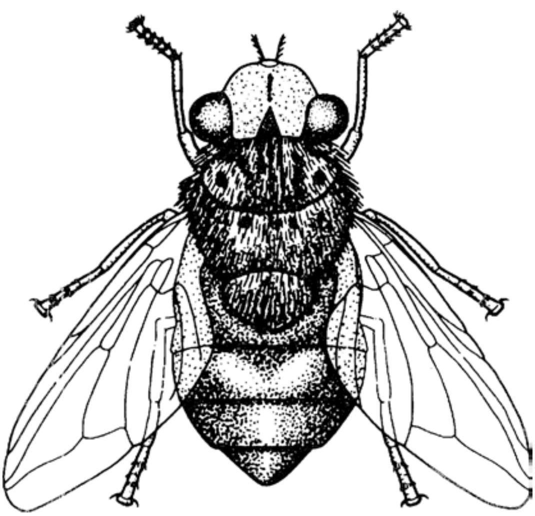


Figure 10.9 Human bot fly (*Dermatobia hominis*) adult.

Life cycle

Dermatobia hominis occurs primarily in lowland forests, being especially common along woodland paths and at the margins of forest and scrub areas. These flies have an interesting and remarkable life history. Females glue 15–40 ***eggs*** to the bodies of other arthropods, such as day-flying mosquitoes (especially of the genus *Psorophora*), house flies, stable flies and *Fannia* species, and occasionally even ticks.

Embryos within the attached eggs mature into first-instar larvae after 4–15 days. They do not hatch, however, until the insect carrying the eggs settles on a human or some other warm-blooded animal to take a blood-meal or, as in the case of house flies, to feed on sweat. Larvae then emerge from the eggs and drop onto the host's skin. Here, within 5–10 minutes, the larvae either enter the skin through the bite puncture or penetrate soft unbroken skin and burrow into the subcutaneous tissues. Each larva produces a boil-like (***furuncular***) swelling which has an opening through which the larva breathes. Occasionally two or three larvae may be found within a single swelling.

First-instar larvae are 1–1.5 mm long, more or less cylindrical in shape (Fig. 10.10a), and have the anterior half of the body covered with numerous ***spines*** of two different sizes. Second-instar larvae are a completely different shape, being enlarged anteriorly but with the posterior half of the body distinctly narrow, giving the appearance of a bottle with a long neck. Relatively large thorn-like ***spines*** encircle the middle segments (Fig. 10.10b). The third and final instar larvae are about 18–25 mm long, more or less oval in outline, and have relatively small ***spines*** on the anterior

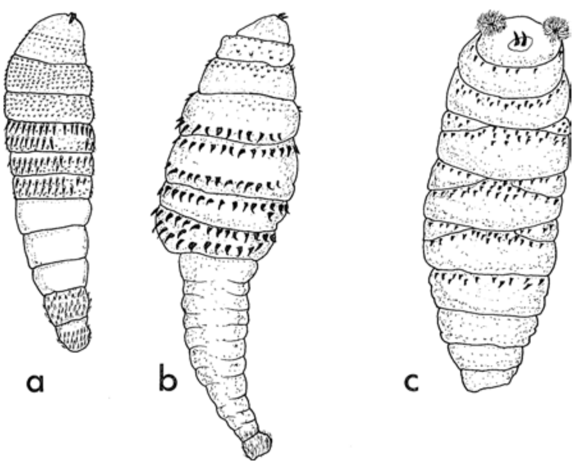


Figure 10.10 Larvae of human bot fly (*Dermatobia hominis*), showing small and larger spines: (a) first instar; (b) second instar; (c) third and final instar.

segments (Fig. 10.10c, Plate 18). A pair of distinct ***flower-like*** spiracles is present anteriorly.

Larval development occurs in a small pocket excavated in the subdermal tissues of the host, and lasts about 4–10 weeks or even longer. Mature larvae wriggle out of the skin and drop to the ground, where they pupate just under the surface of the soil. Adult flies emerge from the puparia after about 4–18 weeks, but are rarely seen.

Medical importance

Larvae of *Dermatobia hominis* invade the subcutaneous tissues of humans on various parts of the body, including the head, arms, abdomen, buttocks, thighs, scrotum and axillae. They produce boil-like (***furuncular***) swellings which suppurate, and this may attract other myiasis-producing flies. They can cause considerable discomfort and pain. The ***long duration*** of the larval life (10 weeks or more) means that infected persons may be encountered in almost any part of the world following air travel.

Because of their numerous spines and their shape, larvae are often difficult to remove by squeezing them out; consequently surgical removal under sterile conditions may be necessary, frequently accompanied by a local anaesthetic.

10.7 Other myiasis-producing flies

The black blowfly (*Phormia regina*), found in North America, Europe and northern parts of Asia, breeds mainly in carrion but sometimes causes facultative myiasis in humans. *Cochliomyia macellaria* is found from North to South America and develops primarily on carrion, but occasionally larvae are found in wounds, and so cause facultative myiasis. However, it is of only minor medical importance.

Several species of flies cause myiasis in livestock, such as sheep and goats (e.g. *Oestrus ovis*), cattle (e.g. *Hypoderma bovis*) and horses and donkeys (e.g. *Gasterophilus haemorrhoidalis*). Occasionally humans become infected with their maggots. Those most likely to suffer are people working with the flies' natural hosts: for example, shepherds looking after sheep may become infected with *O. ovis*.

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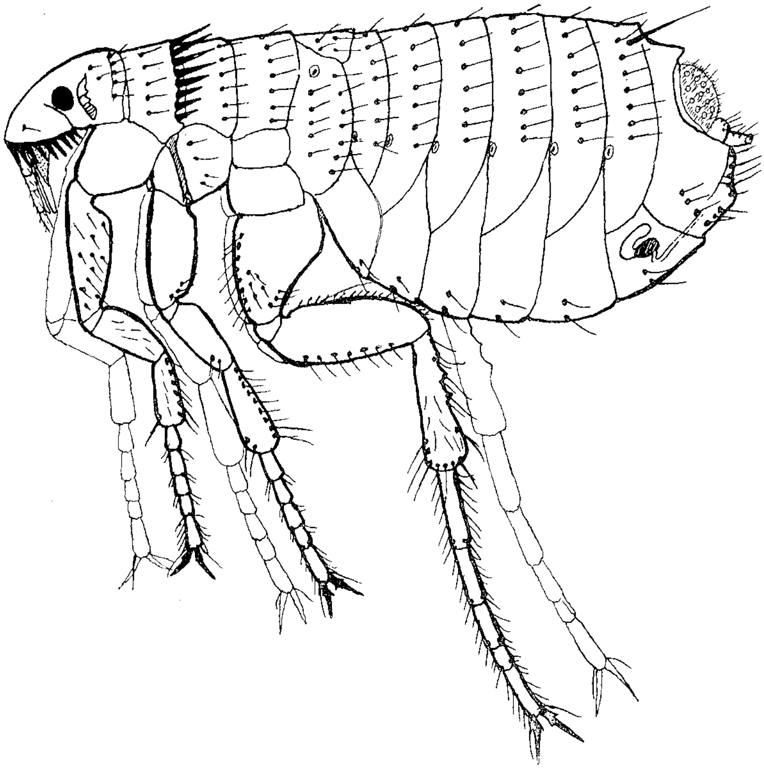
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11

Fleas (Siphonaptera)



There are about 2500 species and subspecies of fleas in about 220 genera, but only relatively few are important pests of humans. About 94% of species bite mammals, while the remainder are parasitic on birds. Fleas occur almost worldwide, but many have a more restricted distribution; for example the genus *Xenopsylla*, which contains important plague vectors, is confined to the tropics and warmer parts of some temperate countries.

Medically the most important fleas are *Xenopsylla* species, such as *X. cheopis*, which is a vector of plague (*Yersinia pestis*) and flea-borne murine typhus (*Rickettsia typhi*). Fleas in the genus *Ctenocephalides* may be intermediate hosts of cestodes (*Dipylidium caninum*, *Hymenolepis diminuta*). Fleas may also be vectors of tularaemia (*Francisella tularensis*), and the chigoe or jigger flea (*Tunga penetrans*) 'burrows' into people's feet.

11.1 External morphology

Adult fleas are more or less oval in shape and relatively small (1–6 mm); they are ***compressed*** laterally and vary from light to dark brown (Plate 19). Wings are absent, but there are three pairs of powerful legs, with the hind legs specialized for jumping. The legs, and much of the body, are covered with bristles and small spines.

The head is approximately triangular, bears a pair of conspicuous eyes (a few species are eyeless), and short three-segmented more or less club-shaped ***antennae*** which lie in depressions behind the eyes. The mouthparts point downwards. In some species a row of coarse, well-developed tooth-like spines, collectively known as the ***genal comb*** or genal ctenidium, is present along the bottom margin of the head (Figs. 11.1, 11.2).

The thorax has three distinct segments: the pro-, meso- and metathorax. The posterior margin of the pronotum (i.e. dorsal part of the prothorax) may have a row of tooth-like spines forming the ***pronotal comb*** or pronotal ctenidium (Fig. 11.1). Fleas in some genera lack both pronotal and genal combs and are referred to as ***combless*** fleas (Fig. 11.2). In some genera fleas have both combs, while in other species the pronotal comb is present and the genal comb absent, but never the reverse (Fig. 11.2). A sternite called the mesopleuron is located above the middle pair of legs. In several genera, including *Xenopsylla*, which contains important plague vectors, this sternite is clearly divided into two parts by a thick vertical rod-like structure called the ***meral rod***, pleural rod, mesopleural suture or just rod. The presence of this rod, combined with the absence of both genal and pronotal combs, indicates the genus *Xenopsylla* (Fig. 11.2). However, it must be stressed that the presence of a meral rod by itself does not identify fleas as *Xenopsylla* species, because fleas in several other genera have combs and a meral rod.

In female fleas the tip of the abdomen is more rounded than in males and is not upturned as in males. Internally in about the sixth to eighth

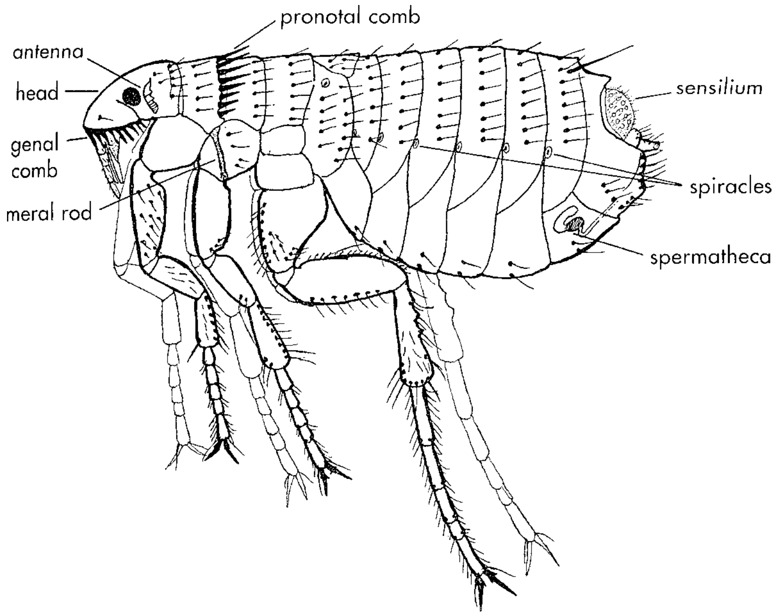


Figure 11.1 Lateral view of an adult flea, showing position of combs and the meral rod (pleural rod).

abdominal segments are one or two distinct brownish spermathecae (Fig. 11.1). However, epidemiologically it is not important to distinguish the sexes because ***both*** take blood-meals and can be vectors. A sensory dome-shaped structure having setae, called the sensilium, is present dorsally on apparent segment 8 and aids fleas in detecting vibrations and temperature changes as well as in host detection.

11.1.1 The alimentary tract of adult fleas

To understand the role fleas have in transmitting plague it is necessary to describe the alimentary tract and the method of blood-feeding.

Saliva, which contains anticoagulants, is injected into the host during feeding. Blood is sucked up through the pharynx and oesophagus into the bulbous ***proventriculus*** (Fig. 11.3), which is provided internally with numerous (250–450) backward-projecting spines. It was previously accepted that these spines prevented the regurgitation of the blood-meal into the oesophagus. However, recent experiments seem to show that regurgitation has little or no effect on disease transmission.

Finally, the blood-meal enters a relatively large stomach (mid-gut), where it is digested. The hind-gut is continuous with a small dilated rectum, which has rectal glands that extract water so that the faeces pass out in a dry state.

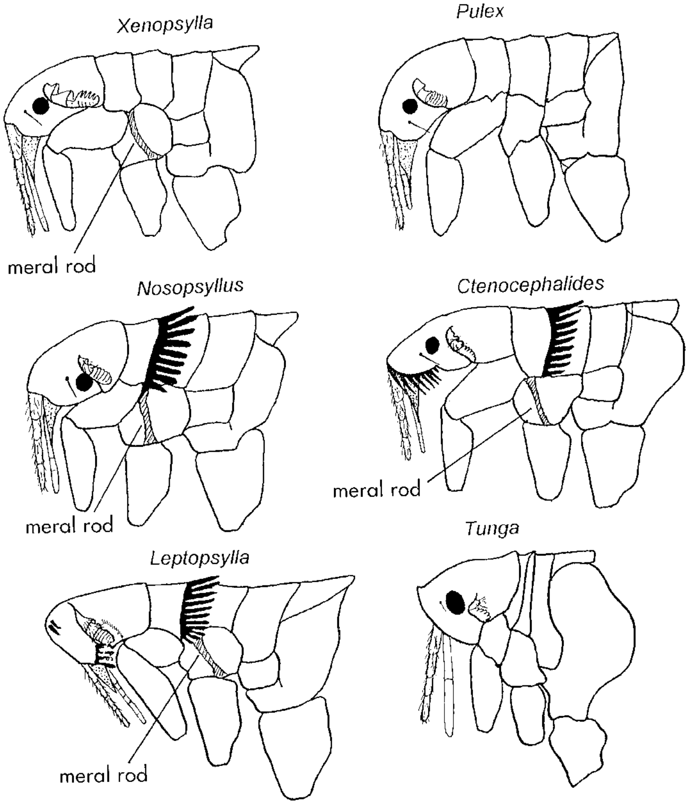


Figure 11.2 Diagrams of the head and thoracic segments of adult fleas, showing how the presence or absence of combs and the meral rod can distinguish six medically important genera.

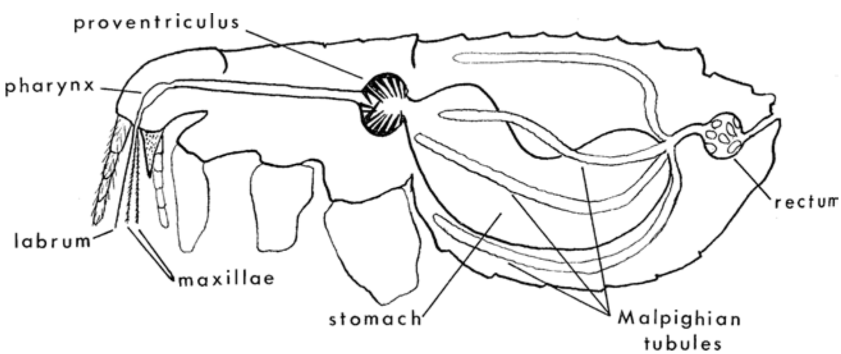


Figure 11.3 Diagrammatic representation of the alimentary canal of an adult flea, showing backward-projecting spines in the proventriculus.

11.2 Life cycle

Both sexes take blood-meals and are therefore equally important as disease vectors. The following account is a generalized description of the life cycle of fleas that feed on humans or animals, such as dogs, cats and commensal rats. The life cycle of the chigoe flea (*Tunga penetrans*) is described separately.

A gravid female rodent flea leaves the host and deposits her eggs in debris which accumulates in the host's dwelling place, such as rodent burrows. Fleas that bite humans or their domestic pets, such as cat fleas, lay their eggs while they are still on the host but because they are not sticky they soon fall off the host and are mainly found in areas where hosts, such as cats or dogs, spend the most time. Eggs are very small (0.1–0.5 mm), oval, white or yellowish and lack any visible pattern. Adults commonly live for 10 days to 6 weeks, but sometimes for 6–12 months or even longer. During her lifetime a female may lay 300–1000 eggs, mostly in batches of 3–25 a day.

Eggs usually hatch after 2–5 days, but this depends on the species of flea, temperature and humidity. A minute legless larva emerges from the egg (Fig. 11.4). It has a small brownish head with a pair of very small antennae, followed by 13 pale brown, distinct and more or less similar segments. Each ***segment*** has a circle of setae near the posterior border. The last segment ends in a pair of finger-like ventral processes termed ***anal struts***. The presence of these struts and setae on the body distinguish larval fleas from other insects of medical importance.

Larvae are very active. They avoid light, and shelter in cracks and crevices and amongst debris on floors of houses, or in nests or animal burrows. Occasionally, however, larvae are found on people who wear dirt-laden clothes, and sometimes in beds. Larvae feed on almost any organic debris, but to successfully achieve adulthood it seems that larvae

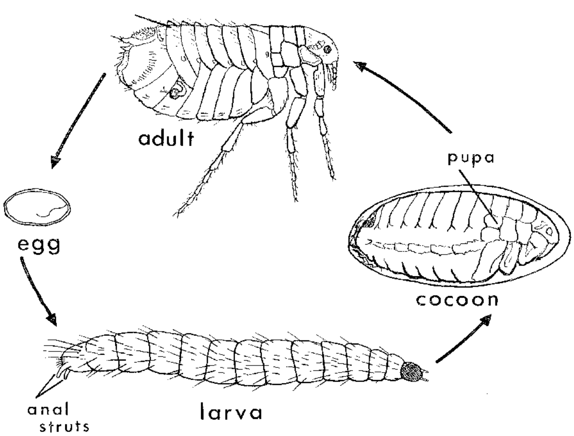


Figure 11.4 Life cycle of a flea.

of many species must consume partly digested blood evacuated from the alimentary canal of adult fleas (i.e. adult flea faeces). There are usually three larval instars, but in a few species there are only two instars (e.g. *Tunga penetrans*, page 185). The larval period is commonly 2–3 weeks, but varies according to species, and may be prolonged to 200 days or more by unfavourable conditions such as limited food supply and low temperatures. Mature larvae are 4–10 mm long. Unlike adult fleas, larvae die if relative humidities are either too low or too high.

At the end of the larval period the larva spins a whitish ***cocoon*** from silk produced by its salivary glands. Being sticky, it becomes covered with fine particles of dust and debris including sand picked up from the floor of the host's home. Consequently cocoons are difficult to distinguish from their surroundings. About 2–3 days after having spun a cocoon around itself the larva pupates within the cocoon. Adults are ready to emerge from the pupa after about 5–14 days, although this period depends on ambient temperature and also a stimulus. This is usually vibrations generated by a host's movements within its home, burrow or nest. If, however, animal shelters or houses are vacated adult fleas remain in their cocoons until their dwelling places are reoccupied. In some species, carbon dioxide emitted from hosts or a seasonal increase in humidity stimulates emergence. Adults may remain alive in their cocoons for ***4–12 months*** or sometimes for over a year. This explains why people moving into buildings which have been vacated for many months may suddenly be attacked by large numbers of newly emerged very bloodthirsty fleas seeking their first blood-meal.

The life cycle from egg to adult emergence may be as short as 2–3 weeks for certain species under optimum conditions, but frequently the life cycle is considerably longer, taking many months.

Fleas avoid light and are usually found sheltering amongst the hairs or feathers of their hosts, or on people under their clothing or even in beds. During feeding fleas eject faeces composed of semi-digested blood of the previous meal and then excess blood ingested during the act of feeding. This mixture of partially digested and virtually undigested blood often marks clothing and bed linen of people heavily infested with fleas.

Although most species of fleas have favourite hosts, they are not entirely host-specific. For example, cat and dog fleas (*Ctenocephalides felis* and *C. canis*) will readily feed on humans, as well as many wildlife species, especially in the absence of their normal hosts. Human fleas (*Pulex irritans*) often feed on dogs and pigs, while rat fleas (*Xenopsylla* species) will attack people in the absence of rats. Most fleas will in fact bite other hosts in their immediate vicinity when their normal hosts are absent or scarce. Although feeding on less acceptable hosts keeps fleas alive, their fertility can be reduced. Fleas rapidly abandon dead hosts to find new ones, behaviour which is of profound epidemiological importance in plague transmission. Some fleas can withstand both considerable ***desiccation*** and prolonged

periods of ***starvation***, for example six months or more, when no suitable hosts are present. However, cat and dog fleas die within 10 days away from their hosts. On a host, fleas move by rapidly crawling, whereas off the host they jump more than crawl in their search for new hosts. Some flea species can jump about 20 cm vertically and 30 cm or more horizontally. Such remarkable feats are achieved through a rubber-like protein called ***resilin***. This is very elastic and can become highly compressed; rapid expansion of the compressed state gives the power for jumping.

11.3 Medical importance

11.3.1 Flea nuisance

Although fleas can be important vectors of disease, the most widespread complaint is their troublesome bites, which may result in considerable discomfort and irritation. The most common nuisance flea is the cat flea (*Ctenocephalides felis*), which has a worldwide distribution. Females often lay up to 25 eggs a day for about a month. Of lesser importance as a pest is the dog flea (*Ctenocephalides canis*) and more rarely the human flea (*Pulex irritans*). The cat flea has become the most common flea on dogs.

Fleas frequently bite people on the ankles and legs, but at night a sleeping person may be bitten on any part of the body. People who become hypersensitive to flea bites can suffer from dermatitis, and inhalation of flea faeces can cause allergies. Children under 10 years tend to experience greater discomfort from flea bites than older people.

Because fleas are difficult to catch this increases the annoyance they cause. People attacked by fleas frequently spend sleepless nights alternately scratching themselves and trying to catch the fleas.

11.3.2 Plague

There are three main types of plague, bubonic, septicemic and pneumonic, all caused by the bacterium *Yersinia pestis*. Medically the most important is bubonic plague, of which there are worldwide about 1000–3000 cases annually in parts of Asia, northwestern and southern Africa, South America and western North America. Bubonic plague is a ***zoonosis***, being primarily a disease of wild animals, especially rodents. About 200 rodent species and 14 lagomorphs (e.g. hares and rabbits) have been shown to harbour plague bacilli. The transmission cycle of plague between wild rodents, such as gerbils, marmots, voles, chipmunks and ground squirrels, is termed ***sylvatic***, campestral, rural or enzootic plague. Many different species of fleas bite rodents and maintain plague transmission amongst them. When people such as fur trappers and hunters handle these wild animals there is the risk that they will get bitten by rodent fleas and become infected with plague.

An important form of plague is ***urban plague***. This describes the situation when plague circulating among wild rodents has been transmitted to commensal rats (e.g. the black rat, *Rattus rattus* and brown (Norwegian) rat, *R. norvegicus*). It is maintained in the rat population by fleas such as *Xenopsylla cheopis* (Europe, Asia, Africa and the Americas), *X. astia* (Southeast Asia) and *X. brasiliensis* (Africa, South America and India). When rats are living in close association with people, such as in rat-infested slums, fleas normally feeding on rats may bite humans. This commonly happens when rats are infected with plague and rapidly develop an acute and fatal septicaemia. On their death infected fleas leave the rats and feed on humans. In this way bubonic plague is spread by rat fleas to human populations.

The most important vector is *Xenopsylla cheopis*, but other fleas such as *X. astia* and *X. brasiliensis* are also plague vectors in some areas. More rarely *Nosopsyllus fasciatus* and *Leptopsylla aethiopica* can be vectors, but these two flea species are reluctant to feed on people and so rarely transmit plague to humans. In addition to humans becoming infected by the bites of fleas that previously fed on infected rats, plague can also be spread from person to person by fleas, such as *Xenopsylla* species and *Pulex irritans*, feeding on a plague victim then on another person. This latter method, however, appears to play a minor role in transmission. *Pulex irritans* may play a more important role in transmission than previously considered, especially in areas not having *X. cheopis*, but it seems that transmission is mainly mechanical, that is through contaminated flea mouthparts.

It is important to understand the methods by which fleas transmit plague. Plague bacilli sucked up by male and female fleas during blood-feeding are passed to the stomach, where they multiply greatly and extend forwards to invade the ***proventriculus***. In some species, especially those in the genus *Xenopsylla*, further multiplication in the proventriculus may result in it becoming partially, or more or less completely, ***blocked*** (Fig. 11.5). In a partially blocked flea, because the proventriculus is not

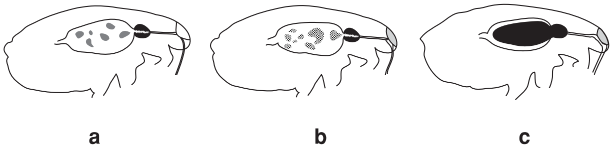


Figure 11.5 Development of *Yersinia pestis* in *Xenopsylla cheopis*: (a) early stage with proventriculus functioning normally; (b) partial blocking, with proventriculus failing to form an efficient valve mechanism; (c) completely blocked flea, with blood not being able to enter the stomach. (Courtesy of Miss M. A. Johnson, and Blackwell Publishing, Oxford, publishers of *Entomology for Students of Medicine* (1962) by R. M. Gordon and M. M. J. Lavoipierre.)

functioning normally, some of the blood that has been sucked into the stomach is regurgitated along with plague bacilli into the host. With completely blocked fleas, blood is sucked up from a host with considerable difficulty about as far as the proventriculus, where it mixes with plague bacilli and is then regurgitated back into the host. Blocked fleas soon become starved and repeatedly bite in attempts to get a blood-meal, and therefore are epidemiologically potentially very dangerous.

Another, but less important, method of infection is by the flea's faeces being rubbed into abrasions in the skin or coming into contact with mucous membranes. Plague bacilli can remain infective in flea faeces for as long as three years. Occasionally the tonsils become infected with plague bacilli due to crushing infected fleas between the teeth!

In septicaemic plague the bacilli are in the blood, and in pneumonic plague they invade the lungs. Very occasionally septicaemic plague is transmitted mechanically by fleas.

11.3.3 Murine typhus

Although murine typhus, also known as endemic typhus or Mexican typhus, occurs almost worldwide, the annual number of human cases has fallen from more than 5000 in 1945 and 1946 to presently just 20–80 cases a year.

Murine typhus is caused by the bacterium *Rickettsia typhi*, which is ingested by a flea with its blood-meal. In the gut the rickettsiae multiply, but unlike plague bacilli they do not block the proventriculus. Transmission occurs when infected ***faeces*** are scratched or rubbed into abrasions or come into contact with delicate mucous membranes, and also by the release of rickettsiae from crushed fleas. Faeces remain ***infective*** for many months to a year or more; under laboratory conditions they have remained infective for 4.5–9 years! Murine typhus is essentially a disease of rodents, particularly rats such as *Rattus rattus* and *R. norvegicus*. It is spread among rats and other rodents by *Xenopsylla* species, especially *X. cheopis*, but also by *Nosopsyllus fasciatus* and *Leptopsylla segnis*. A few ectoparasites which are not fleas are vectors, such as the spined rat louse (*Polyplax spinulosa*) and possibly the cosmotropical rat mite (*Ornithonyssus bacoti*).

People become infected mainly by the faeces of *Xenopsylla cheopis*, but occasionally species such as *Nosopsyllus fasciatus*, *Ctenocephalides canis*, *C. felis* and *Pulex irritans* may be involved in transmission. *Leptopsylla segnis* does not bite humans, but it is possible that murine typhus is sometimes spread to people by an aerosol of this flea's infective faeces.

Rickettsiae of murine typhus can pass to the flea's ovaries and subsequently to the eggs, larvae and adults, that is ***transovarial*** transmission. But whether this is epidemiologically important remains uncertain.

Rickettsia felis was first detected as a human pathogen in 1994, but it is very similar to *R. typhi*; in fact polymerase chain reaction (PCR) techniques

are required to separate these two species, so infections of *R. felis* may have often been missed. *Rickettsia felis* has been isolated in the USA from opossums (*Didelphis* species) and cat fleas (*C. felis*) which feed on them. It seems there is an urban type of murine typhus involving *R. typhi*, rats and rat fleas (described above) and a rural type involving *R. felis*, opossums and cat fleas which can also be transmitted to humans. The infection can be maintained in cat fleas by vertical transmission for at least 12 generations.

11.3.4 Cestodes

Dipylidium caninum is the commonest tapeworm of dogs and cats, and it occasionally occurs in children. It can be transmitted by fleas (*C. felis, C. canis* and *P. irritans*) to both pets and humans as follows. Tapeworm proglottids containing eggs excreted by a pet crawl away from the host and dry on exposure to air. Larval fleas feeding on organic debris in host bedding bite into the dried proglottids, releasing the eggs, which they then swallow. Larval worms hatching from the ingested eggs penetrate the gut wall of the larval flea and enter the body cavity (coelom). They remain trapped here before passing to the pupa and finally to the adult flea, where they encapsulate and become cysticercoids (infective larvae). Animals become infected by licking their coats during grooming and swallowing infected adult fleas. Similarly, young children fondling and kissing dogs and cats can become infected by swallowing cat and dog fleas, or by being licked by dogs which have crushed infected fleas in their mouths, thus liberating the infective cysticercoids.

The rat tapeworms *Hymenolepis diminuta* and *H. nana* have similar life cycles.

11.3.5 Less important diseases

Cat-scratch disease (CSD) caused by *Bartonella henselae* is transmitted among cats by cat fleas. It seems that cats' claws are contaminated with *Bartonella*-infected flea faeces and that transmission to humans is mainly by cat scratches. Tularaemia (*Francisella tularensis*) may occasionally be transmitted to humans by flea bites. Ticks, however, are the main vectors, and it must be stressed that the role of fleas as vectors of these two infections is minimal.

11.4 *Tunga penetrans*

Tunga penetrans is found in the Caribbean, Central and South America and sub-Saharan Africa including Madagascar. It is increasingly found in travellers returning home from tropical countries. *Tunga penetrans* is sometimes referred to as the chigoe, jigger flea or sand flea. *Tunga penetrans* does not transmit any disease but is a nuisance because females become imbedded in the skin.

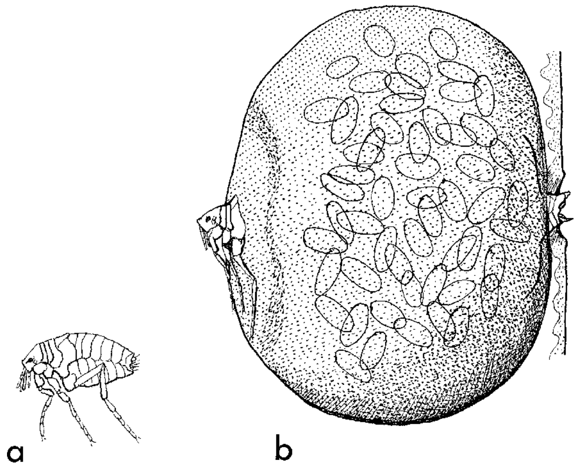


Figure 11.6 Adults of *Tunga penetrans* (chigoe flea): (a) non-gravid female; (b) gravid female with enormously swollen abdomen full of eggs which is embedded in the skin of a host. Note (on right) that the tip of the abdomen projects from the host's skin to the exterior.

11.4.1 External morphology

Adults of both sexes are exceedingly small, only about 1 mm long (Fig. 11.6a, Plate 20). They have ***neither*** genal nor pronotal combs and are easily separated from other fleas of medical importance by their very ***compressed*** first three (thoracic) segments, and by the paucity of spines and bristles on the body.

11.4.2 Life cycle and medical importance

Eggs of *Tunga penetrans* are dropped onto the floor of houses or on the ground outside, and hatch in about 3–4 days. Larvae inhabit dirty and dusty floors or dry sandy soils, especially in areas frequented by hosts of the adult fleas. There are two instars, not three as in most flea species, and under favourable conditions larval development is completed within about 10–14 days; the pupal period lasts about 5–14 days.

Newly emerged adults jump and crawl on the ground until they locate a host, usually a person or pig. ***Both sexes*** feed on blood, but whereas the male soon leaves the host after taking a blood-meal, the female, after being fertilized, 'burrows' into the skin where it is soft, such as between the toes or under toenails. Strictly speaking she does not burrow, but the host's skin envelops her. Other areas of the foot, including the sole, may also be invaded. In people habitually sitting on the ground, such as beggars or infants, the buttocks may be infested, and particularly large infestations have been recorded from leprosy patients. In heavily infested individuals

the arms, especially the elbows, may also be attacked, and occasionally the females 'burrow' into the soft skin around the genital region. The entire flea, with the exception of the tip of the abdomen bearing the anus, genital opening and large respiratory spiracles, becomes ***completely buried*** in the host's skin, and here she continues to feed. The area surrounding the embedded flea becomes very itchy and inflamed, and secondary infections may become established, resulting in ulcerations and accumulation of pus. While the blood-meal is being digested, the abdomen distends to an enormous size, and after 8–10 days the flea is both the shape and size (6 mm) of a small pea (Fig. 11.6b). The abdomen now contains thousands of minute eggs, and over the next 7–14 days about 150–200 eggs are laid each day, most of which eventually fall to the ground and hatch after about 3–4 days. The life cycle from egg to adult usually takes 4–6 weeks but can be as short as 18 days.

After female fleas die they remain ***embedded*** in the host. This frequently causes inflammation and may result in secondary infections, which if ignored can lead to loss of the toes, tetanus, or even gangrene. Male fleas cause no such trouble, as they do not 'burrow' into the skin.

Chigoe fleas are most common in people not wearing shoes, such as children. Up to 100 lesions have been found in the feet of a single child in endemic areas, and there are commonly 40 or more lesions per person. Because these fleas are feeble jumpers, wearing shoes is a simple method of reducing the likelihood of flea infestation.

Females embedded in the skin can be removed with fine needles under aseptic conditions, and the wounds should then be treated with antibiotics and dressed. They are best removed within the first few days of their becoming established, because when they have greatly distended abdomens, containing numerous eggs, they are difficult to extract without rupturing them, and this increases the risk of infections. Surgical extractions, however, are not easy and it may be better to treat lesions topically with lotions of ivermectin or metrifonate (trichlorfon) on two consecutive days to kill fleas in situ.

Pigs, in addition to humans, are commonly infested with *Tunga*, and may provide a local reservoir of infestation. Other animals such as cats, dogs and rats are also readily attacked.

11.5 Control of fleas

Repellents such as DEET or permethrin-impregnated clothing may afford some personal protection against fleas.

Insecticide resistance has been reported in cat fleas, human fleas and *Xenopsylla* species to one or more of the following categories of insecticides: organochlorines, organophosphates, carbamates, pyrethrins and pyrethroids. Nevertheless, insecticides remain the main tool for flea control, although there is increasing reliance on insect growth regulators (IGRs).

11.5.1 Rodent fleas

Both adults and larvae of rodent fleas can be killed by using hand-operated dusters to apply insecticidal dusts such as carbamates, pyrethroids or organophosphates to rodent burrows and their nearby runways. Treatment with carbamates and pyrethroids can remain effective for 2–4 months in dry conditions. Rodent fleas in houses can be controlled by spraying floors with bendiocarb, malathion or pyrethroids, or fogging with permethrin or pirimiphos-methyl.

Controlling fleas in urban outbreaks of plague or murine typhus requires extensive and well-organized insecticidal operations. While insecticides are being applied, rodenticides formulated as baits, such as the anticoagulants warfarin and brodifacoum, can be used to kill rodents. If there is resistance to these rodenticides then the fast-acting anticoagulants such as bromadiolone and chlorophacinone can be used, but it is then ***essential*** to apply these several days after insecticidal applications. Otherwise rodents will be killed before their fleas are killed, and the fleas will then bite other mammals including people, which may result in increasing disease transmission. Where there is resistance to warfarin and other anticoagulants, calciferol, a fast-acting rodenticide, can often be substituted.

Although IGRs appear to have good potential for control of plague fleas, they have received relatively little evaluation.

11.5.2 Cat and dog fleas

Cat and dog fleas (*Ctenocephalides felis* and *C. canis*) can be detected by examining the fur on the neck or stomach of the hosts. Powders, sprays or spot-on concentrates of insecticides such as bendiocarb, pyrethroids and organophosphates and also IGRs can be applied to the animal's fur. Dusts are safer than liquids because they are less likely to be absorbed through the animal's skin and cause unpleasant side reactions. Increasingly IGRs such as pyriproxyfen, methoprene and lufenuron can be applied to the animal's skin or formulated as a pill to be given orally, or by injection. With IGRs fleas will still lay eggs but either they will fail to hatch or the emerging larvae will fail to develop. Such treatments may be effective for 3–6 weeks. Flea collars impregnated with insecticides or IGRs are not very effective.

However, an important consideration is that most fleas are found away from the host, not on it. Typically there may be only about 25 adult fleas on a cat, but on the floor and bedding, apart from a few adult fleas, there may be 500 cocoons and as many as 3000 larvae and 1000 eggs. Clearly, control measures should also be applied to beds, kennels and other places where pets sleep. These items should either be treated with insecticidal powders or lightly sprayed with malathion, chlorpyrifos, one of the pyrethoids or an IGR. Cocoons, however, will not be killed, although the emerging adults will be. Duration of effective control depends on the types of materials

sprayed (e.g. earthen or wooden floors, synthetic or woollen carpets), but IGRs generally remain effective longer than conventional insecticides, some giving good control for about 2–4 months..

Vacuum cleaning floors, carpets and pets' bedding can also be very effective in removing the immature stages of fleas.

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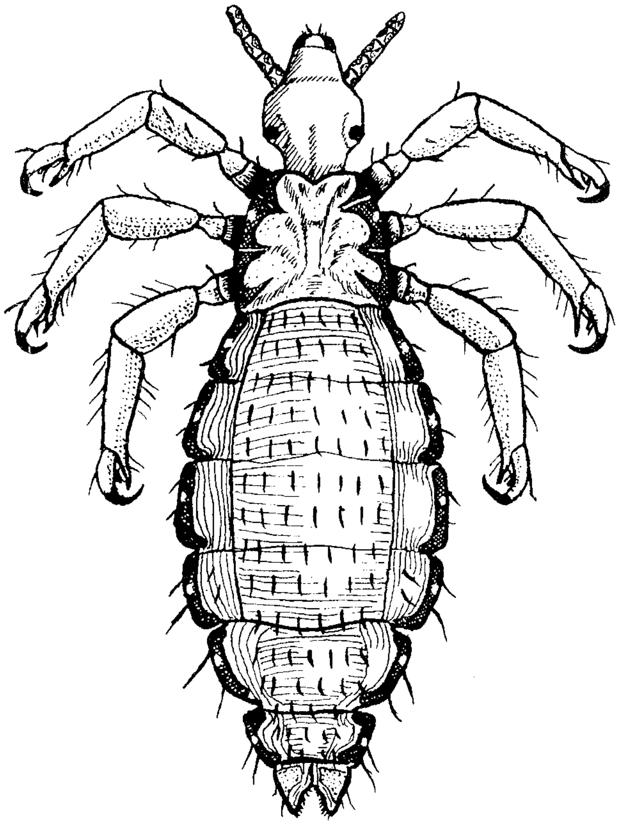
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12

Sucking lice (Anoplura)



Three types of blood-sucking lice occur on humans, the body louse (*Pediculus humanus*), the head louse (*Pediculus capitis*) and the pubic or crab louse (*Pthirus pubis*). Morphologically the body and head lice are virtually ***indistinguishable***. In the laboratory the two can interbreed but there is very little evidence they do this outside the laboratory, and here they are treated as two distinct species, although many regard the head louse as a subspecies of the body louse. All three species of lice have a more or less worldwide distribution, but they are often more common in temperate areas.

Body lice are vectors of louse-borne typhus (*Rickettsia prowazekii*), trench fever (*Bartonella quintana*) and louse-borne relapsing fever (*Borrelia recurrentis*).

12.1 The body louse (*Pediculus humanus*)

12.1.1 External morphology

Adults are small, pale beige or greyish wingless insects, with a soft but rather leathery integument, and are ***flattened*** dorsoventrally (Fig. 12.1, Plate 21). Males measure about 2–3 mm and females about 3–4 mm. The head has a pair of small black eyes and a pair of short five-segmented antennae. The three thoracic segments are fused together and the legs are

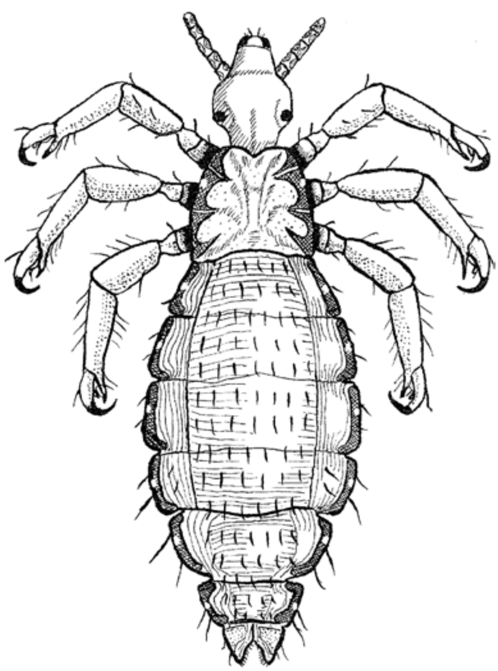


Figure 12.1 Dorsal view of body louse (*Pediculus humanus*). The head louse (*P. capitis*) looks virtually identical.

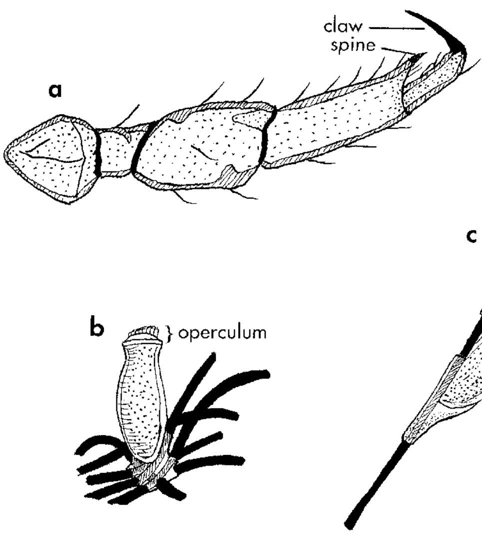


Figure 12.2 Head louse (*Pediculus capitis*) and body louse (*P. humanus*): (a) leg of a body louse, showing tarsal claw and tibial spine; (b) unhatched egg of a body louse glued to fibres of clothing; (c) one hatched (upper) and two unhatched (lower) eggs of the head louse cemented to a hair. For convenience these three eggs are shown very close together, but in practice they are rarely this close on a head hair.

stout and well developed. The short thick tibia has apically a small ***spine*** on its inner side, and the short tarsus ends in a curved ***claw*** (Fig. 12.2a). Hairs of the host, or clothing, are gripped between this tibial spine and tarsal claw.

Mouthparts of the louse differ from those of most blood-sucking insects in that they do not form a projecting proboscis, but consist of a sucking snout-like projection called the ***haustellum***, which is armed on the inner surface with minute teeth that grip the host's skin during feeding. Needle-like stylets are thrust into the skin and saliva is injected into the wound to prevent blood from clotting. Blood is sucked up and passes into the stomach for digestion.

The lateral margins of the abdominal segments are sclerotized and often appear darker than the rest of the segments.

In males there are dark transverse bands on the dorsal surface of the abdominal segments and the tip of the abdomen is rounded, whereas in females it is ***bifurcated*** and used to grip fibres of clothing during egg-laying.

12.1.2 Life cycle

Both sexes take blood-meals, and feeding occurs at any time during the day or night. Both adults and immature stages live permanently on humans,

clinging mainly to fibres of their clothing and usually only to body hairs during feeding. Female lice glue about 6–10 eggs per day very firmly on clothing fibres, especially on those along the seams of underclothes, such as vests and pants, but also on shirts and very occasionally on body hairs. The egg, commonly called a ***nit*** (though some apply this term only to the hatched egg), is oval, white, about 1 mm long, and has a distinct ***operculum*** (cap) containing numerous small perforations which give the egg the appearance of a minuscule pepper pot (Fig. 12.2b). Intake of air through these holes not only supplies the tissues of the developing embryo with oxygen but aids hatching in the following way. Just prior to hatching, the fully developed louse within its eggshell swallows air, which distends the body against the eggshell, thus building up a back pressure causing the head of the louse to be pushed up against the operculum and forcing it off. Female lice live for 2–4 weeks and may lay 150–300 eggs.

The egg stage lasts about 5–11 days, except that eggs on discarded clothing may not hatch until 2–3 weeks; or in cool conditions not at all. Because eggs cannot survive longer than four weeks there is little danger of acquiring body lice from clothing not worn for over a month.

Lice have a ***hemimetabolous*** life cycle. The louse hatching from the egg is termed a ***nymph*** and resembles a small adult. It takes a blood-meal and passes through three nymphal instars, and after about 7–14 days becomes an adult male or female louse. Duration of the nymphal stages depends on whether clothing is worn continuously. If it is discarded at night and nymphs are subjected to lower temperatures, this may slow their development. A louse usually takes 3–5 blood-meals a day from its host. The life cycle from egg to adult is about 2–3 weeks.

The body louse is an ectoparasite of humans. Away from humans, unfed lice die within 2–4 days, but blood-fed individuals may survive for 5–10 days. On their hosts, blood-feeding adults probably live for about 30 days. Lice are very sensitive to changes in temperature. They quickly abandon a dead person to seek new hosts. They also leave a person with a high temperature, being unable to feed at temperatures above about 40 °C.

A very heavily infested person may have 400–500 lice on his or her clothing and body. In very exceptional conditions some 20 000 lice have been recorded from a single person! Usually, however, less than 100 lice are found on any one individual, and many have considerably fewer than this.

Body lice are spread by close contact and are especially prevalent under conditions of overcrowding and in situations where people rarely wash or change their clothes. They are therefore commonly found on people in primitive jails, in refugee camps and in trenches during wars, and also after disasters such as floods or earthquakes when people are forced to live in very overcrowded, and usually insanitary, conditions. People living in mountainous areas in East Africa, Ethiopia, Sudan, Burundi, Nepal, India and Andean regions of South America, where cold weather necessitates

wearing several layers of clothes which may be rarely changed or washed, often have lice. In more developed countries body lice are found mainly on homeless people, and infestations may reach a peak in cold weather when several layers of woollen underclothes are worn.

12.1.3 Medical importance

Pediculosis

Presence of body, head or pubic lice on a person is sometimes referred to as ***pediculosis***. The skin of people who habitually harbour large numbers of body lice may become pigmented and tough, a condition known as vagabond's disease, hobo disease or sometimes as morbus errorum.

Because lice feed several times a day, saliva is repeatedly injected into individuals, and its toxic effects may cause weariness, irritability or a pessimistic mood: the person feels lousy. Some people develop allergies such as dermatitis or severe itching, or have a type of asthmatic bronchitis. Secondary infections such as impetigo, which is very contagious, can also result from large numbers of biting lice.

Louse-borne epidemic typhus

Rickettsiae of louse-borne typhus, *Rickettsia prowazekii*, are ingested with blood-meals taken by both male and female lice, and also by their nymphs. They invade the epithelial cells lining the stomach of the louse and multiply enormously, causing the cells to become greatly distended. About four days after the blood-meal the ***gut cells*** rupture and release the rickettsiae back into the lumen of the insect's intestine. Due to these injuries the blood-meal may seep into the haemocoel of the louse, giving the body a reddish colour. Rickettsiae are passed out in the ***faeces*** of the louse, and people become infected when these are rubbed or scratched into abrasions, or come into contact with delicate mucous membranes such as the conjunctiva. Infection can also be caused by ***inhalation*** of the very fine powdered dry faeces. Also, if a louse is crushed, such as by persistent scratching, rickettsiae in the gut are released and may cause infection through abrasions etc. Rickettsiae can remain infective in dried louse ***faeces*** for about 60 days.

Humans, therefore, become infected with typhus either by the faeces of the louse or by crushing it, not by its bite. An unusual feature of louse-borne epidemic typhus is that it is a disease of the louse as well as of humans. Rupturing of the intestinal epithelial cells caused by multiplication of the rickettsiae frequently kills the louse after about 8–12 days. This may explain why people suffering from typhus are sometimes found with remarkably few, or no, lice on their bodies or clothing. Epidemic typhus is much less common than previously. However, an outbreak of epidemic typhus occurred in Russia in 1997, and in 1999 5600 cases were reported from

China. However, the disease mainly occurs in cool mountainous regions of Africa, Asia, and Central and South America.

People are usually considered to be the reservoir hosts of typhus. Those who have recovered from an infection often harbour *R. prowazekii* in their lymph nodes and later, sometimes after more than 30 years, the rickettsia may reinvade other body cells. Such ***recrudescence*** of typhus is termed Brill–Zinsser disease. This can occur many years after the primary attack, and may lead to the spread of epidemics.

Louse-borne epidemic relapsing fever

Borrelia recurrentis is ingested with the louse's blood-meal from a person suffering from epidemic relapsing fever, but within about 24 hours all spirochaetes have disappeared from the lumen of the gut. Many have been destroyed, but the survivors have passed through the stomach wall to the ***haemocoel***, where they multiply to reach enormous numbers after 10–12 days. The accepted way that someone can be infected is by the louse being crushed and the released spirochaetes entering the body through abrasions or mucous membranes, or less commonly through intact skin. The habit of crushing lice between the fingernails, or the less desirable habit of killing them by cracking them with the teeth, is clearly dangerous if lice are infected with relapsing fever or typhus. Recently, it has been shown that faeces of infected lice can contain live *B. recurrentis*, and so transmission may also involve the faeces.

Louse-borne relapsing fever has disappeared from Europe but remains common in Central and East Africa, Sudan, Ethiopia, Afghanistan and Peru. Ethiopia has about 1000–5000 cases annually; this is about 95% of worldwide infections. As with *R. prowazekii*, infection is ultimately fatal to the louse.

Trench fever

Trench fever is a relatively uncommon and non-fatal disease which was first recognized during World War I (1914–18) among soldiers in the trenches, and then reappeared in eastern Europe during World War II (1939–45). The disease disappeared again, only to reappear later in North America and Europe in the 1980s, occurring mainly in homeless people and those who were HIV-positive. In the 1990s and 2000s it was also reported from many parts of the world, including the USA, Canada, Mexico, Peru, Bolivia, France, Japan, China, Australia, North Africa, Burundi and other sub-Saharan countries.

Trench fever is caused by *Bartonella quintana*. The bacteria are ingested by the louse during feeding and become attached to the walls of the gut cells, where they multiply. They do not penetrate the cells, as do typhus rickettsiae, and consequently they are not injurious to the louse. After 5–10

days the ***faeces*** are infected. Like typhus, the disease is conveyed to humans either by crushing the louse or by its faeces coming into contact with skin abrasions or mucous membranes. Bacteria persist for many months, possibly even a year, in dried louse faeces, and it is suspected that infection may also commonly arise from ***inhalation*** of the dust-like faeces. The disease may be contracted by those who have no lice, but are handling louse-infected clothing contaminated with faeces.

12.1.4 Control

If louse-infested clothing is subjected to a minimum temperature of 70 °C for at least an hour body lice are killed. In epidemic situations, however, such measures may be impractical and immediate reinfestation may occur, so insecticides are usually used for louse control.

Lice are killed when insecticidal dusts, such as carbaryl, propoxur, malathion or permethrin, mixed with an inert carrier (e.g. talc), are blown by a plunger-type duster between a person's body and his or her underclothes. However, checks should firstly be made to determine whether lice in the area have developed resistance to any of the insecticides to be used.

Impregnation of clothing with a pyrethroid insecticide may provide long-lasting protection against louse infestations, and such treated clothing may remain effective after several washings. Probably the best pyrethroid for this is permethrin

Trials have shown that orally administered ivermectin kills body lice, and also head lice, but it is not yet universally approved for control of human lice.

12.2 The head louse (*Pediculus capitis*)

12.2.1 External morphology

Only very minor morphological differences separate body and head lice (Plate 22). In practice, these differences are not very important because lice found on clothing or on the body are invariably body lice, whereas those on the head are head lice.

12.2.2 Life cycle

The life cycle is very similar to that of the body louse, except the eggs (***nits***) are not laid on clothes but are cemented to the hairs of the head, especially at their base (Fig. 12.2c), and normally hatch after 6–7 days. Usually a single egg is laid on each hair. The distance between the scalp and the furthest egg glued to a hair may provide an approximate estimate of the duration of infestation, on the basis that a human hair grows about 1 cm per month. However, eggs may also be laid on long hairs when they are near or

touching the scalp, so that unhatched eggs may be some distance from the base of the hair. Only very occasionally are eggs laid on hairs elsewhere on the body.

Most infected individuals have only 10–20 head lice, but in very severe infestations the hair may become matted with a mixture of nits, nymphs, adults and exudates from pustules resulting from bites of the lice. In such cases bacterial and fungal infections may become established, and an unpleasant crust may form on parts of the head, underneath which are numerous head lice. Empty, hatched ***nits*** remain firmly cemented to the hairs of the head. A female lays about 6–8 eggs per day, amounting to about 50–150 eggs during her lifetime, which is about 2–4 weeks. Eggs hatch within 5–10 days and the duration of the nymphal stages is about 7–10 days. Away from people head lice die within 2–3 days.

As with body lice, dissemination of head lice is only by close contact, such as children playing together with their heads frequently touching. Girls often have more head lice than boys because they have more intimate play, with their heads frequently touching, and also because girls often play with their friends' hair. Infestations are often more common in women than in men, but are usually highest in children. Outbreaks of head lice often occur when people are crowded together, such as in prisons or refugee camps. Catching head lice from inanimate objects such as hats, scarves or chair backs is considered unlikely.

12.2.3 Medical importance

In many areas of the world head lice are a serious public health problem, and in many countries prevalence has been increasing. In some schools in the USA and the UK almost 50% of pupils have head lice. Often there are higher infestation rates in overcrowded homes and where hygiene is poor. There is little evidence that head lice are natural vectors of the diseases transmitted by body lice – for example, typhus epidemics are always associated with body lice – but they may occasionally be minor vectors in some outbreaks of louse-borne relapsing fever.

12.2.4 Control

Regular combing with an ordinary comb, although not removing the eggs, may reduce the number of nymphs and adults. A plastic ***louse comb*** with very closely set fine teeth is much better but may not remove all lice and their eggs. Alternatively, the head can be shaved!

Most commercial preparations for controlling head lice contain pyrethroids such as phenothrin or permethrin, or organophosphates such as malathion. Insecticidal formulations include dusts, emulsions and lotions. The choice depends on the availability of proprietary brands,

preference of patients and costs. Although insecticidal dusts are efficient, they are not acceptable to most people because they give the head a greyish appearance, signalling that the person has lice. Shampoos which are applied and then washed off after a few minutes are not usually very effective. Some commercial preparations proclaim that lotions need only remain on the head for 10 minutes or two hours, but it is better to leave the insecticidal lotion on the head for about 12 hours, e.g. overnight, before washing it off.

Although some insecticides, such as malathion and permethrin, are reputed to be ovicidal, a ***second*** treatment after 7–10 days is recommended whatever insecticide is used, because it is difficult to kill all eggs with just a single application. None of the compounds will remove eggs cemented to the hairs, but these can be removed with a louse comb. As lice are readily transmitted between people, it is recommended that all members of a household are treated, not just those detected as having lice.

Insecticide resistance, especially to the pyrethroids, is widespread and is the main reason for the increase in head louse infestations worldwide, but a novel treatment consists of dimethicone (a common commercial name is Hedrin), and this is now widely used in many countries. It is usually formulated as a 4% lotion, and is normally sprayed on the head. It is not a conventional insecticide but a silicone compound that coats the lice and kills them by suffocation. After about an hour the hair can be combed with a louse comb to remove dead lice and their eggs, after which the hair can be washed. Retreatment after seven days kills newly hatched lice from residual eggs. It is unlikely that resistance will evolve against dimethicone, as it is not a typical insecticide. Presently Hedrin is not cheap, and it may be too expensive for poorer communities.

Trials using orally administered ivermectin show that the drug kills both head lice and body lice, but it is not yet universally approved for control of human lice.

12.3 The pubic louse (*Pthirus pubis*)

12.3.1 External morphology

The pubic louse is smaller (1.3–2 mm) than *Pediculus* species and is easily distinguished from them. In the pubic louse the body is nearly as broad as long, making it almost round. Whereas all three pairs of legs are more or less of equal size in the body and head louse, in the pubic louse the middle and hind-legs are much thicker than the front legs and have massive claws (Fig. 12.3, Plate 23). Presence of a ***broad squat*** body and ***very large*** claws, together with more sluggish movements, has resulted in the pubic louse being aptly called the crab louse.

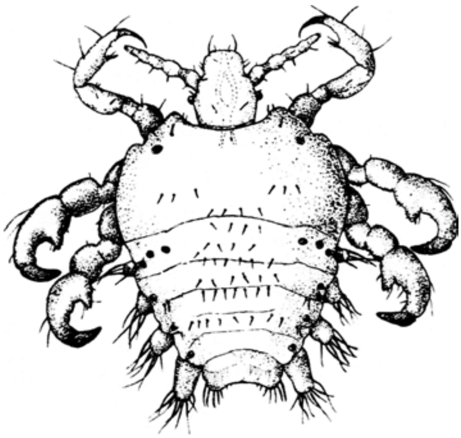


Figure 12.3 Dorsal view of pubic louse (*Pthirus pubis*), showing very large claws on mid- and hind-legs.

12.3.2 Life cycle

Females lay about three eggs a day, totalling some 150–200 in their lifetime. They are slightly smaller than those of the body and head louse and are cemented to the coarse hairs of the genital and perianal regions of the body, and unlike head lice several eggs may be laid on a single hair. Pubic lice may be found on other areas of the body having coarse and not very dense coverings of hair, for example the beard, moustache, eyelashes, underneath the arms and occasionally on the chest, but they are very rarely found on the finer hair of the scalp. Eggs take about 6–8 days to hatch and the duration of the three nymphal stages is about 10–17 days; consequently the life cycle is about 16–25 days. Adults can live up to 30 days.

Pubic lice are considerably less active than *Pediculus*. Infestation with crab lice is usually through sexual intercourse, and characteristically the French call them '*papillons d'amour*'. However, it is wrong to suspect that this is the only method. Young children sleeping with parents can catch crab lice from them, and infestations can arise from discarded clothing, infested bedding, or even ***rarely*** from lavatory seats. Adults survive two days or less away from their hosts.

12.3.3 Medical importance

Although in the laboratory pubic lice can transmit louse-borne typhus, there is little evidence that under natural conditions they spread any disease to humans, although it has been suggested that they have been responsible for typhus outbreaks in China. Severe allergic reactions (***pruritus***) can develop in response to their bites, due to the injection of saliva and the deposition of faeces around the feeding sites. Small characteristic bluish spots (***maculae***

caeruleae) may appear on infested parts of the body. Infestations of pubic lice are sometimes known as pediculosis pubis or phthiriasis (note that, unlike the generic name of the louse, this is spelt with a 'phth').

12.3.4 Control

Originally control involved shaving pubic hairs from the body, but this method has been replaced by the application of insecticidal lotions.

Basically insecticides used for head louse control can be used against pubic lice. Application of 1% permethrin or 5% malathion should kill nymphs and adults and possibly eggs, but a ***second*** application 7–10 days later is advisable in case some eggs are not killed. It may be advisable to treat all hairy areas of the body below the neck. ***Aqueous***, not alcoholic, insecticidal solutions should be used, otherwise irritation may arise due to sensitivity of the genital region. Although resistance to pyrethroids has been reported, insecticide resistance in pubic lice appears to be rare. Infestations on the eyelashes can be treated by applying a small amount of a vaseline ointment or petroleum jelly twice a day for 8–10 days, after which the lice can be carefully pulled off.

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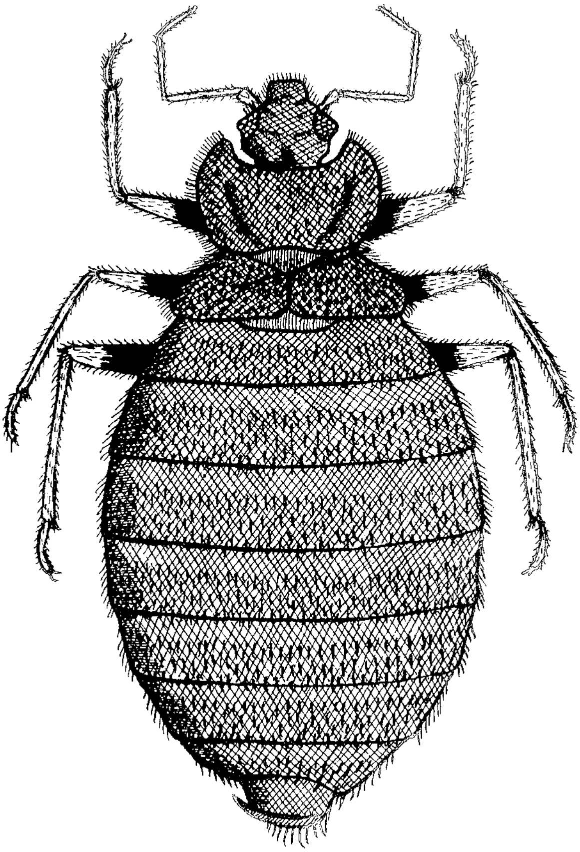
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13

Bedbugs (Cimicidae)



The family Cimicidae includes bedbugs, of which two common species feed on humans. *Cimex lectularius* is widely distributed in tropical and non-tropical countries while *C. hemipterus*, commonly called the tropical bedbug, is essentially a species of the Old and New World tropics although it can also occur in warm areas of some non-tropical countries, such as in Florida, USA. It is not easy to separate these two species, but in *C. lectularius* the prothorax is generally 2.5 times as wide as long, whereas in *C. hemipterus* it is only about twice as wide as long. Also, the abdomen is more rounded in *C. lectularius* than in *C. hemipterus*.

A third species, *Leptocimex boueti*, is found mainly in West Africa but has also been recorded in South America. This species bites bats and also people, but is much less important as a pest than the *Cimex* species.

Infestations of bedbugs have increased since the 1990s in many countries, possibly due to increased global travel. For instance, after the 2000 Olympic Games nearly every hotel in Sydney was infested with bedbugs. Other factors include insecticide resistance and warmer houses. Bedbugs are not considered important vectors, but in addition to constituting a biting nuisance they have been reported as causing iron deficiency in infants.

13.1 External morphology

Adult bedbugs are oval, wingless insects which are ***flattened*** dorsoventrally (Fig. 13.1, Plate 24). They are about 5–7 mm long and when unfed pale yellow or brown, but after a full blood-meal they become a characteristically darker 'mahogany' brown. The head is short and broad and has a pair

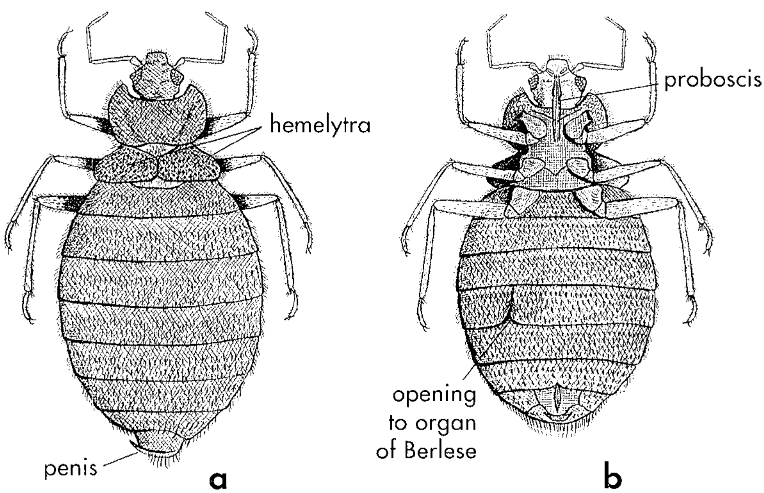


Figure 13.1 Bedbug (*Cimex hemipterus*): (a) dorsal view of adult male; (b) ventral view of adult female.

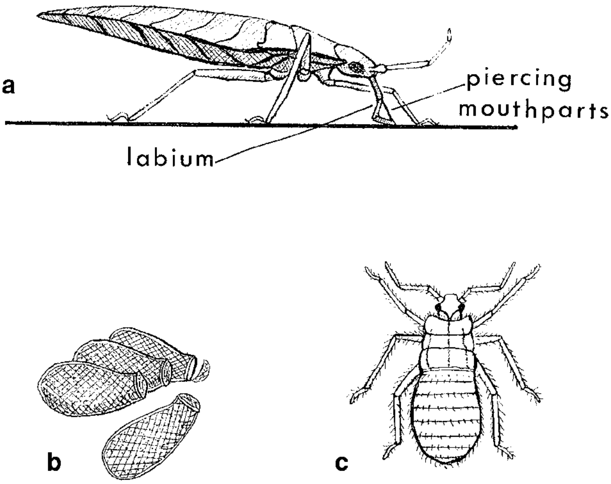


Figure 13.2 Bedbugs: (a) diagram of an adult with proboscis swung forward for blood-feeding; (b) one hatched and three unhatched eggs; (c) first-instar nymph.

of prominent compound eyes, in front of which is a pair of four-segmented antennae. The proboscis is slender, and is normally held closely appressed under the head and prothorax, but when the bug takes a blood-meal it is swung forward and downwards (Fig. 13.2a). The ***prothorax*** is much larger than the meso- and metathorax and has distinct wing-like expansions. Two rudimentary and non-functional more or less oval wing pads, termed ***hemelytra***, overlie the meso- and metathorax. The three pairs of legs are slender but well developed.

The abdomen has 11 segments but only eight are readily visible. In adult males the tip of the abdomen is slightly more pointed than in females, while closer examination shows a small well-developed curved penis (Fig. 13.1a). In females there is a small incision ventrally on the left side of the apparent fourth abdominal segment (Fig. 13.1b). This opens into a special pouch (= sinus) called the mesospermalege, organ of Berlese or organ of Ribaga, which collects and stores sperm. Because both male and female bugs bite it is not medically very important to distinguish the sexes.

13.2 Life cycle

Both sexes of bedbug take blood-meals and are equally important as pests. Feeding usually occurs at night on sleeping people, often just before dawn. If, however, bedbugs are starving they will feed during the day, especially in darkened rooms. Unlike lice, bedbugs do not remain on people but stay only to take blood-meals. Very occasionally, however, in temperate climates they may remain on vagrants who rarely change their clothes. In the

absence of people bedbugs will feed on other hosts, including rabbits, rats, mice, bats, poultry and other birds. During the day adults and nymphs are ***inactive*** and hide in dark and dry places, such as cracks and crevices in furniture, walls, ceilings or floorboards, underneath seams of wallpaper and between mattresses and beds. At night adults and nymphs emerge to feed on sleeping people, after which they return to their resting sites to digest their blood-meals. Bedbugs are gregarious and are frequently found in large numbers. They can move quite rapidly when disturbed.

Females lay about 2–4 eggs a day in cracks and crevices of buildings and furniture, but egg-laying ceases at 13 °C or lower. Eggs are about 1 mm long, pearly white or yellowish white, covered with a very fine and delicate mosaic pattern, and characteristically slightly ***curved*** anteriorly (Fig. 13.2b). Females live several weeks to many months, and occasionally a year or more, and during this time they may lay 150–540 eggs.

Eggs usually hatch after about 8–11 days, but as soon as 4–6 days in warmer houses. If, however, temperatures in houses are low, hatching may be delayed for several weeks, and such unhatched ***eggs*** can survive for three months. During hatching the small ***operculum*** (cap) is pushed from the anterior end of the egg, but often remains partially attached. Empty eggshells usually remain cemented in place after hatching. Newly hatched bedbugs (***nymphs***) are very pale yellow and resemble adults, but are much smaller (Fig. 13.2c). The life cycle is ***hemimetabolous*** and there are five nymphal instars each lasting 3–10 days. The nymphal period lasts 2–7 weeks, but is greatly extended in cool conditions or if regular blood-feeding is prevented by lack of hosts. The life cycle, from egg to adult (Fig. 13.3), can be just 3–4 weeks if temperatures are high and food plentiful, but is more usually 6–10 weeks. In the laboratory ***adults*** can live for four years, and survive more than a year without blood-feeding, but survival is dependent on temperature and humidity.

The method of mating in bedbugs is unique among insects. The penis penetrates the integument and enters the mesospermalege (organ of Ribaga or organ of Berlese) situated on the ventral surface of the female abdomen. Sperm introduced into this 'copulatory pouch' (= sinus) pass into the haemocoel and then ascend the oviducts to fertlize the eggs.

Bedbug ***infestations*** can be detected by the presence of live bugs, cast-off nymphal skins, and hatched and unhatched eggs, all of which may be found in cracks and crevices. In addition, small dark brown or black marks may be visible on bed sheets, walls and wallpaper: these are the bedbug's excreta and consist mainly of excess blood ingested during feeding. Houses with large bedbug infestations may have a characteristic rather sickly smell, but in practice this may not be apparent because the weak odour can be masked by stronger insanitary smells.

Because bedbugs lack wings they do not disperse far, although occasionally they crawl from one building to another. Bedbugs are usually spread to

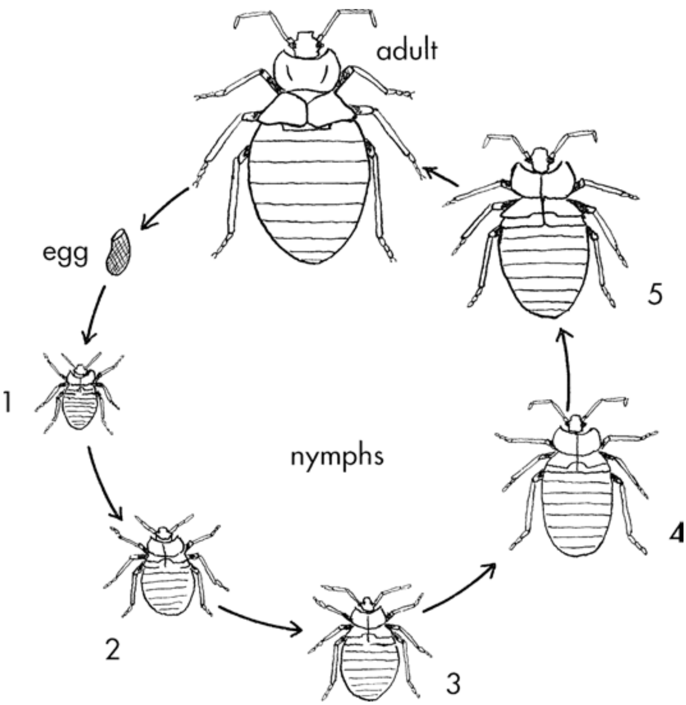


Figure 13.3 Life cycle of bedbugs.

new houses by being introduced with furniture and bedding, or more rarely with clothing and hand baggage. Buying secondhand furniture can result in the introduction of bedbugs into houses.

13.3 Medical importance

Although hepatitis B virus and 27 other pathogens have been recorded in bedbugs there is no evidence that they can transmit any infections to people. They are therefore not considered as vectors.

In areas with dilapidated buildings and poor hygiene standards, bedbug infestations can cause considerable distress. Some people show little or no reaction to their bites, but others may suffer severe reactions and have sleepless nights. Repeated feedings of large numbers of bedbugs can cause iron deficiency in infants and some elderly people.

13.4 Control

Insect repellents and insecticide-impregnated bed-nets can give considerable personal protection against bedbugs.

Floors and walls of infested houses, together with as much furniture as possible, should be sprayed with the carbamate bendiocarb, organophosphates such as malathion, a range of pyrethroids including cypermethrin and also insect growth regulators (IGRs) such as methoprene. If pyrethroids are not being used in spraying then the addition of pyrethrins, or synthetic pyrethroids, can help flush out bedbugs from their hiding places, so increasing their contact with the insecticide used. Mattresses and wooden slats across beds can be dusted with insecticidal powders or lightly sprayed with insecticides, but must be aired afterwards to allow them to dry out completely before being re-used. Bedclothes and infants' mattresses should ***not*** be treated with insecticides. If bedclothes are infested they should be washed in hot water then ironed or dried in the sun. Alternatively clothes can be placed in sealed plastic bags and placed in a freezer (–18 °C) for 24 hours to kill the bedbugs.

Commercially available small insecticidal smoke bombs containing insecticides, such as permethrin, which burn for up to 15 minutes, can be used to fumigate infested premises.

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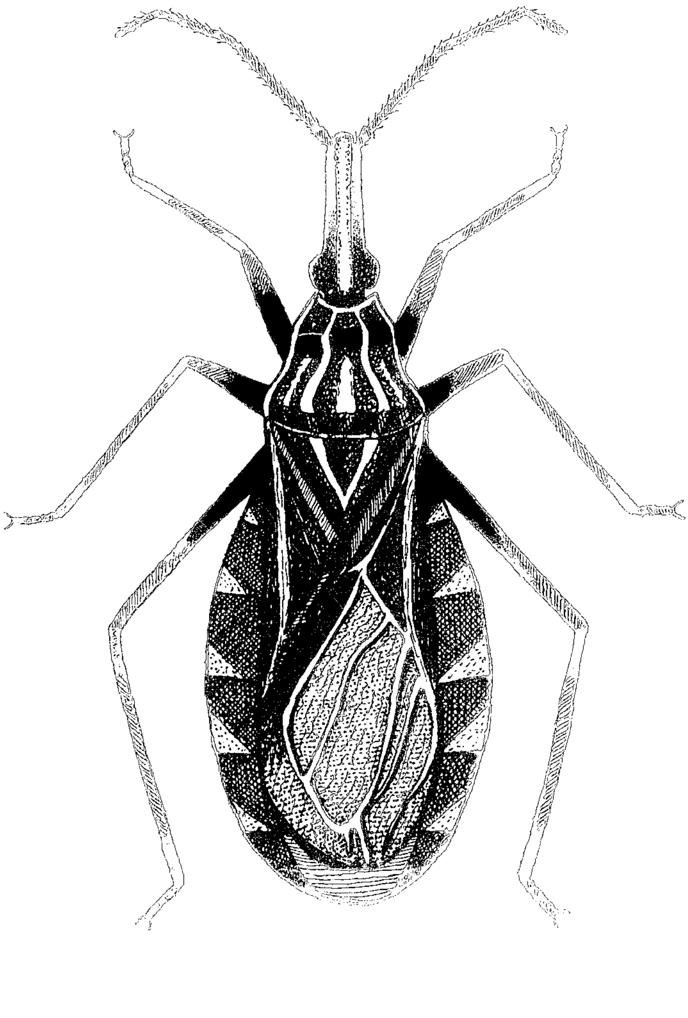
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14

Triatomine bugs (Triatominae)



Blood-sucking bugs in the family Reduviidae belong to the subfamily Triatominae and comprise more than 138 species in 15–17 genera (the number depending on whose authority is accepted). The most important are *Triatoma infestans*, *T. dimidiata*, *Rhodnius prolixus* and *Panstrongylus megistus*, all of which spread Chagas disease (*Trypanosoma cruzi*) in Central and South America. Some can also transmit *Trypanosoma rangeli*, a non-pathogenic organism.

Most Triatominae occur in the Americas, from the Great Lakes of the USA to southern Argentina, but 13 species are found in the Old World tropics. All medically important species are, however, confined to the southern USA, Central and South America. Triatomines are commonly called kissing-bugs, cone-nose bugs, vinchucas or barbeiros.

14.1 External morphology

Triatominae vary from 5 to 45 mm in length, but most are 20–30 mm long. They are easily recognized by their long ***snout-like*** head having a pair of prominent dark-coloured eyes, in front of which is a pair of ***laterally*** situated, long and thin four-segmented ***antennae*** (Fig. 14.1, Plate 25). The proboscis, sometimes called the rostrum, is relatively thin and straight and, as in bedbugs, lies closely appressed to the ventral surface of the head (Fig. 14.2a). However, when the Triatominae take a blood-meal the proboscis is swung forward and downwards (Fig. 14.2b).

The dorsal part of the first thoracic segment of the Triatominae consists of a very conspicuous triangular ***pronotum*** (Fig. 14.1). The meso-and metathorax are hidden dorsally by the folded fore-wings, called ***hemelytra***. The basal part of each hemelytron is thickened and relatively hard, whereas the more distal part is membranous (Fig. 14.3). Hind-wings are entirely

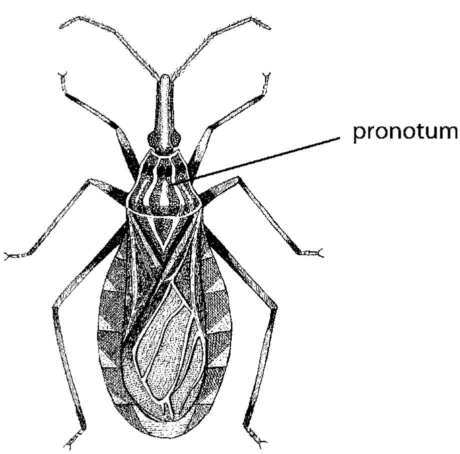


Figure 14.1 Adult *Rhodnius* species, an example of a triatomine bug.

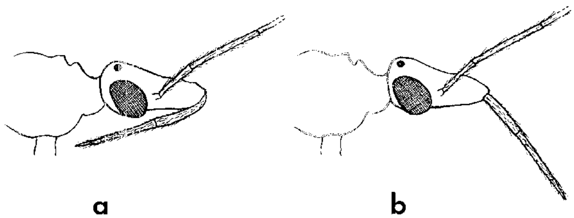


Figure 14.2 Lateral views of the head of a *Triatoma* species: (a) proboscis closely appressed to ventral side of the head; (b) proboscis swung forward in a blood-feeding position.

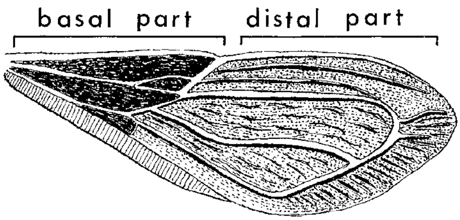


Figure 14.3 Fore-wing (hemelytron) of a triatomine bug, showing thickened basal part and more membranous distal part.

membranous, but when the bug is not flying they remain hidden underneath the hemelytra. The relatively long and slender legs end in paired small claws.

The 11-segmented abdomen is more or less oval in shape but is mostly hidden by the wings, except for the lateral margins, which are bent upwards slightly and are visible dorsally.

Triatominae are frequently a brown-black colour, but some species are more colourful, having contrasting yellow, orange, pink or red markings, usually as bands on the pronotum, basal part of the fore-wings, legs or abdominal margins.

14.2 Life cycle

Eggs are about 1.5–2.5 mm long, oval in shape, but have a slight constriction before the ***operculum*** (cap) (Fig. 14.4). They have a smooth or ornate shell which is pearly white, pink or yellowish depending on the species. Eggs are deposited in cracks and crevices in walls, floors, ceilings and furniture of houses, especially dilapidated mud-walled and thatched-roofed houses in rural areas, or slums at the edge of towns. Some species lay their eggs in rodent burrows and other shelters used by mammalian hosts upon which they feed. Avian feeders deposit their eggs in birds' nests or on leaves of trees. Typically females lay 1–2 eggs a day. The total number

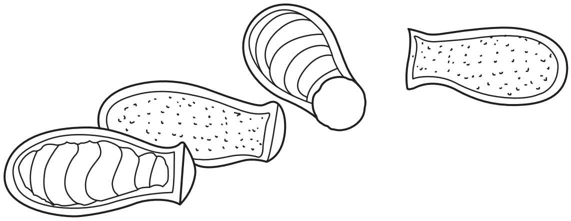


Figure 14.4 Two hatched and two unhatched triatomine eggs.

laid varies from 50 to 1000, depending on the species, their longevity and the number of blood-meals they take, but it is usually 200–300.

The life cycle is ***hemimetabolous***. Small pale ***nymphs***, which resemble adults but lack wings, may hatch from eggs after only 10–15 days, but the incubation period may extend to 37 or rarely up to 60 days. Newly emerged nymphs usually remain hidden in cracks and crevices for 2–3 days before they blood-feed. There are five nymphal instars, each requiring at least one blood-meal before it changes into the succeeding instar. Rudimentary wing pads are visible in the fourth and fifth nymphal stages, but only adults have fully developed wings. ***Young nymphs*** can ingest 6–12 times their own weight of blood, and their abdomens may become so greatly distended that they resemble blood-red balloons. Successive instars take relatively less blood, so that the fifth and last nymphal stage takes about 3–5 times its own weight of blood, while adults ingest 2–4 times their weight of blood. Adults of some species ingest 300–400 mg of blood at each meal and feed every 4–9 days! Sometimes hungry nymphs and adult bugs pierce the swollen abdomens of freshly engorged nymphs and take a blood-meal from them, without apparently causing harm.

Nymphs and adults of ***both sexes*** feed at night on their hosts, and ***feeding*** often lasts 10–25 minutes. People covered with blankets are bitten on any exposed parts of the body, but especially on the nose and around the eyes and mouth. Biting is usually relatively painless and does not awaken people, although some species cause considerable discomfort and there may be prolonged after-effects. Many bugs defecate during or soon after feeding, and this behaviour is very important in the transmission of Chagas disease. Presence of bugs in houses is often characterized by finding shed skins (exuvia) from moulting nymphs and streaks of whitish or dark faecal deposits on walls and furniture.

Because of the relatively long time required to digest their large blood-meals, the ***life cycle*** from egg to adult can take 3–10 months. With large triatomine species the life cycle may last 1–2 years. In the absence of hosts, older nymphs and adults can survive 4–6 months of starvation.

Triatomine bugs in the Americas inhabit both forests and drier areas. Many species feed on wild animals, such as armadillos (*Dasypus* species), iguanas (e.g. *Iguana* species), opossums (*Didelphis* species), rats, marsupials,

ground squirrels (Sciuridae), skunks (Mustelidae), bats, as well as birds. Adults and nymphs of ***sylvatic*** *Triatoma* species shelter in the burrows or nests of these animals, as well as fallen logs, tree-holes and caves. In addition to these ***sylvatic*** species, some bugs have become highly domesticated. Such ***peridomestic*** species feed on donkeys, cattle, goats, horses, pigs, cats, dogs and especially chickens, which in some areas may be particularly important hosts. Several species commonly bite humans, and such ***domestic*** species often live in man-made structures including houses, especially primitive ones made of wood, mud and thatch. Sylvatic species sometimes move into houses as forests are cut down and people occupy previously uninhabited areas. Some species are partly sylvatic and partly domestic in their feeding and resting habits.

If hosts vacate their shelters or homes, hungry nymphs crawl out and seek new hosts, whereas adults fly out to find new hosts and shelters. Some species are attracted by lights into houses.

14.3 Medical importance

14.3.1 Chagas disease

In rural areas of the Americas there can be hundreds of triatomine bugs in a house, and this can be very stressful to the occupants, who will receive many bites during the night. Typically blood loss can exceed 2 ml per person per night, so it is not surprising that large bug populations can contribute to ***anaemia***. Mild hypersensitivity may develop in some people, being expressed as oedema, pruritus or erythema.

However, the main importance of the Triatominae is that they transmit *Trypanosoma cruzi*, the causative agent of Chagas disease, sometimes referred to as South American trypanosomiasis. ***Trypomastigotes*** ingested with a blood-meal undergo their entire development within the ***gut*** of the bug. They develop into ***epimastigotes*** and greatly multiply, and after 8–17 days become infective metacyclic trypomastigotes in the lumen of the hindgut. ***Blood-feeding*** commonly lasts 10–25 minutes or longer, and during this time, or soon afterwards, many species of bugs excrete liquid or semi-liquid faeces which may be contaminated with the metacyclic forms of *T. cruzi* derived from a previous blood-meal. People become infected when ***excreta*** is scratched either into skin abrasions or into the site of the bug's bite, or when it gets rubbed into the eyes or other mucous membranes. If the bug's bite produces local irritation causing the person to scratch, this facilitates infection. ***Transmission*** is not by the bite of the insect, only through its faeces.

About 70 triatomine species have been recorded naturally infected with *T. cruzi*, but in practice only about 20 species living in very close association with people, and therefore regularly feeding on them, are important

vectors. Such vectors include *Triatoma infestans* (Ecuador southwards to Argentina), *Panstrongylus megistus* (Brazil, Bolivia, Paraguay, Argentina and Uruguay), *Rhodnius prolixus* (Guatemala, Honduras, Nicaragua, Guyana, Surinam, French Guiana, Colombia and Venezuela) and *T. dimidiata* (Mexico to Ecuador and Peru). Efficiency of a vector will depend on its speed of feeding and whether it defecates on a person during feeding.

Chagas disease is a ***zoonosis***. *Trypanosoma cruzi* is essentially a parasite of wild animals, such as opossums, armadillos, many species of wild and urban rats and mice, squirrels, carnivores, monkeys and possibly bats, all of which may serve as ***reservoir hosts***. The ***triatomine bug*** itself can also be a reservoir of infection, but in some areas humans are considered to be the principal reservoir host. Apart from acquiring *T. cruzi* through a bug's faeces, some animals become infected by eating the bugs or infected animals, as in the case of carnivores that have fed on rodents infected with *T. cruzi*. Rarely people can also acquire infection by eating infected meat (e.g. inadequately cooked opossums) or food contaminated with excrement of infected bugs.

Infection rates of Triatominae are often exceptionally high. For example, it is not uncommon to find infection rates of about 25%, or even 50% or more. Even higher infection rates (78%) have been found in *Triatoma protracta* in California, but because this species very rarely bites people it is not considered a vector to humans. Vectors account for more than 80% of transmission; blood transfusion (17%) and congenital transmission (2%) also occurs.

14.3.2 Trypanosoma rangeli

Another trypanosome is *Trypanosoma rangeli*, which occurs from Mexico to Brazil but is non-pathogenic in humans. It is transmitted by triatomines, especially by *Rhodnius prolixus*. In the vector the trypanosomes undergo dual development: some of the metacyclic infective forms migrate to the hind-gut while others penetrate the gut wall, pass across into the haemocoel and then migrate to the salivary glands. People are mainly ***infected*** by the bug's bite and only rarely by its faeces.

14.4 Control

Control of Chagas disease is mainly by spraying the interior surfaces of walls and roofs/ceilings of houses, outhouses, chicken sheds and goat pens with residual insecticides. Although fenitrothion (organophosphate) is sometimes used, pyrethroids are the most commonly sprayed insecticides, particularly deltamethrin, cyfluthrin and lambda-cyhalothrin. Careful surveillance detects whether after a year there is reinfestation or foci of bugs that need further spraying. Resistance to several insecticides, including some pyrethrioids, has been recorded, but presently this does not hinder

control operations. Insecticidal smoke bombs which when lit dispense pyrethroid insecticides are sometimes used in houses to alleviate biting.

Bug populations can be reduced by making houses unattractive as resting sites: for example, by plastering walls to cover up cracks in which the bugs might hide, and by replacing dilapidated mud and thatched houses with those built of bricks or cement blocks and having corrugated metal roofs. However, because of the high costs of building new houses, rehousing has yet to be carried out on a large scale.

The above methods will destroy bugs resting in houses but are less effective against those resting in natural outdoor shelters. Such peridomestic populations sometimes invade houses.

14.4.1 Southern Cone Initiative

In 1990 the World Health Organization (WHO) estimated there were about 18 million people in Latin America who were infected with Chagas disease and 100 million at risk of infection, but these numbers have been reduced since the initiation in 1991 of an extensive vector control programme.

In 1991 Argentina, Bolivia, Brazil, Chile, Paraguay and Uruguay, joined in 1996 by Peru, proposed a plan of action to eliminate the main vector, *Triatoma infestans*, chiefly by vector control methods such as insecticidal spraying of houses.

In 1997 Uruguay was declared free of Chagas disease transmission, as was Chile in 1999 and Brazil in 2005. Other countries, especially Bolivia and Peru, are moving towards interrupted transmission of Chagas. In 1997 two new initiatives were launched to reduce transmission, one in the Central American countries of Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua and Panama, the other to cover the Andean countries of Colombia, Venezuela, Peru and Ecuador. However, as two of the main vectors in these two regions, *Triatoma dimidiata* and *Rhodnius prolixus*, are not so endophilic, indoor residual spraying is not so effective. At present there is little information on the success of these two initiatives.

Clearly the target of the WHO to eliminate Chagas disease in Latin America by 2010 has not been achieved. In 2008 it was estimated that there were still more than 25 million people at risk of Chagas disease. However, the fight against Chagas disease continues.

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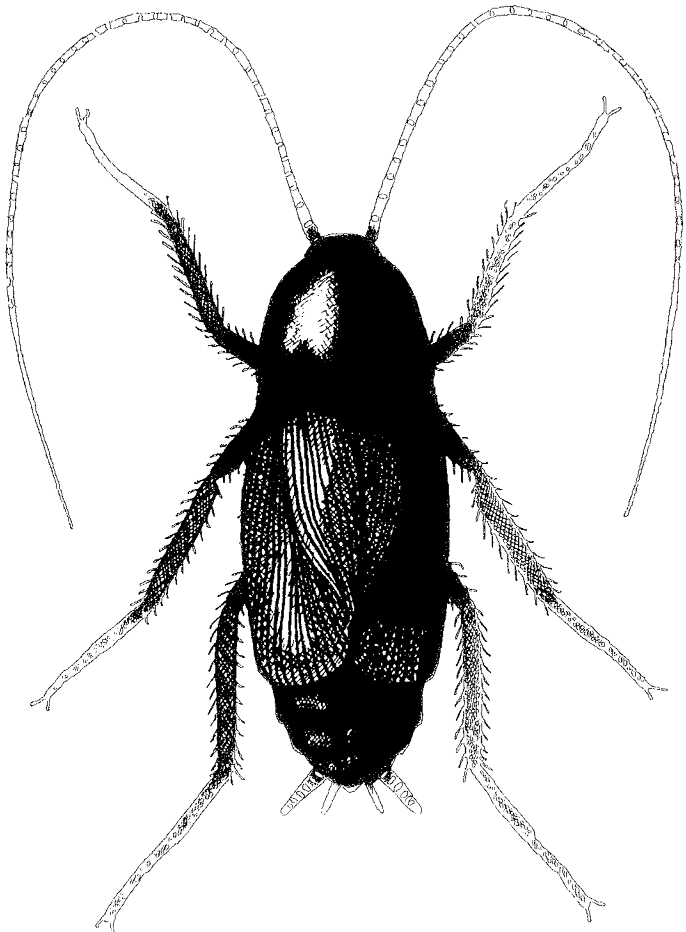
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15

Cockroaches (Blattaria)



Cockroaches belong to the order Blattaria, and there are about 4000 species of which 20–30 are serious domestic pests. The most important medically are *Blattella germanica* (the German cockroach), *Blatta orientalis* (the oriental cockroach), *Periplaneta americana* (the American cockroach), *P. australasiae* (the Australian cockroach) and *Supella longipalpa* (the brown-banded cockroach). Cockroaches are sometimes called roaches or steambugs. They have an almost worldwide distribution.

Cockroaches aid in the mechanical transmission of various pathogenic viruses, bacteria and protozoans.

15.1 External morphology

The more common household pest species are chestnut brown or black, 10–50 mm long, flattened dorsoventrally, and have a smooth, shiny and tough integument. The head is small and sometimes almost hidden by the large, rounded ***pronotum***. A pair of long and prominent filiform ***antennae*** arise from the front of the head between the eyes (Fig. 15.1, Plate 26). Cockroach mouthparts are developed for chewing, gnawing and scraping; they cannot suck blood. Both sexes have two pairs of wings. In some household species ***wings*** in the female are shorter than those of the male, and female *Blatta orientalis* has very small non-functional wings. The cockroach fore-wings, called ***tegmina***, are thick and leathery. They are not used in flight but are protective covers for the membranous hind-wings, which when not in use are folded shut, fan-like, over the body. Although the hind-wings are used for flying, cockroaches rarely fly. The well-developed legs

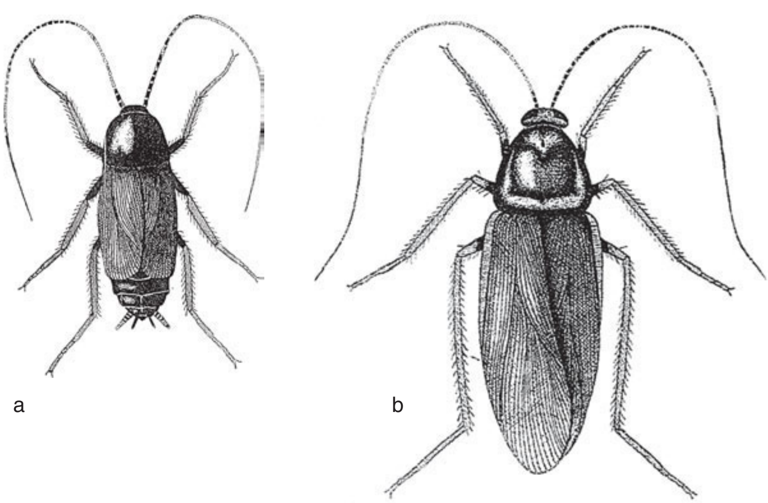


Figure 15.1 Adult cockroaches: (a) *Blatta orientalis* (oriental cockroach); (b) *Periplaneta americana* (American cockroach).

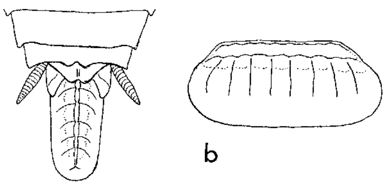


Figure 15.2 (a) Ootheca protruding from the abdomen of *Blatella germanica* (German cockroach); (b) lateral view of a typical cockroach ootheca.

are covered with prominent small spines and bristles; the five-segmented tarsi end in a pair of claws.

The segmented abdomen is more or less oval, and depending on species is either completely or partly hidden by the folded overlapping wings. In both sexes a pair of prominent segmented pilose ***cerci*** arise from the last abdominal segment (Fig. 15.2a), although in some species they are hidden from view by the wings.

Cockroaches are often mistaken for beetles (order Coleoptera) but they can be distinguished by having the ***fore-wings*** placed over the abdomen in a closed scissor-like manner. In beetles the fore-wings (elytra) meet dorsally to form a distinct line down the centre of the abdomen. In addition, the elytra of beetles are generally thicker than the tegmina of cockroaches.

15.2 Life cycle

Cockroaches like warmth, and in temperate countries they often hide behind radiators and hot-water pipes during the ***day***. In warm countries they are found in almost any dark place, such as cesspits, septic tanks, sewers, refuse tips, dustbins, cupboards, underneath chairs, tables, sinks, baths and beds, behind refrigerators and cooking stoves. They are common in kitchens, especially when food is left out overnight, and in restaurants, hotels, bakeries, breweries, laundries and aboard ships. They are also frequently common in hospitals. Cockroaches are ***nocturnal*** and are rarely seen during the day unless they are disturbed from their hiding places. They become very active at night, running over floors, tables and other furniture to seek food. When lights are suddenly switched on cockroaches can be both seen and heard scuttling along.

They are ***omnivorous*** and voracious feeders, eating any type of food. They also eat paper, clothes (particularly starched ones), books, wallpaper, dried blood, sputum, excreta, dead insects, in fact almost any animal or vegetable matter. They may gnaw the fingernails and toenails of babies and sleeping or comatose people, and even infest the hair of vagrants.

Cockroaches habitually disgorge partially digested meals and deposit their excreta on almost anything, including food. They can ***live*** for 5–10 weeks without water and for many months without food, but this is not an important limiting factor because they very rarely occur in areas where food is not available. Young nymphs, however, may die within about 7–10 days in the absence of food.

Eggs are laid encased in a brown bean-shaped case called an ***ootheca*** (Fig. 15.2b), which can contain 5–50 eggs but typically 12–40. Cockroaches, especially *Blattella germanica*, are often seen running around with an ootheca partly protruding from the tip of the abdomen (Fig. 15.2a). Oothecae are deposited in cracks and crevices in dark and secluded places, and in some species are cemented to surfaces, such as the undersides of tables, chairs and beds.

Cockroaches live for many months to two or more years, and during this time females will lay 4–90 oothecae, varying according to species.

Cockroaches have a ***hemimetabolous*** life cycle. Nymphs hatch from eggs after about 1–3 months, the time depending on both temperature and species. Young nymphs are very pale and delicate versions of the adults, whereas the older ones are progressively darker and more like the adults. Nymphs are wingless; the wings gradually develop with ensuing nymphal instars, but only adults may have fully developed wings. The number of nymphal stages is variable within and between species. There are commonly between ***five and seven nymphal stages*** but there may be as many as 13, such as sometimes in *Periplaneta americana*. Duration of the nymphal stage varies according to temperature, abundance of food and species. It commonly lasts 2–3 months in *Blattella germanica*, 12–15 in *Blatta orientalis*, and 10–14 in *Periplaneta americana*, but occasionally up to 23 months.

Cockroaches spread very rapidly from infested houses to adjoining ones. They often gain entry by climbing up water pipes and waste pipes. They are also spread as oothecae, nymphs and adults in furniture and other belongings.

15.3 Medical importance

15.3.1 Allergies

Only relatively recently has the importance of cockroach allergies been recognized. About half of asthmatics are allergic to cockroaches, their cast-off skins or excreta, while about 10% of non-asthmatic people will exhibit cockroach allergies. Symptoms include sneezing, skin reactions, sore eyes, recurrent ear infections and in extreme cases shortness of breath. The allergic rate is second only to that caused by house-dust mites (Chapter 20).

15.3.2 Infectious agents

Because of their dirty habits of feeding indiscriminately on both excreta and foods, and excreting and regurgitating partially digested meals over food, the presence of cockroaches in houses, hotels and hospitals is, not surprisingly, highly undesirable!

Most parasitic infections isolated from cockroaches are also spread directly from person to person without the aid of intermediary insects, so it is usually difficult to prove that cockroaches are responsible for any disease outbreak. Nevertheless, because of their insanitary habits they have been suspected as aiding the transmission of various pathogens. For example, more than 40 bacterial infections have been isolated from cockroaches, including *Entamoeba histolytica*, *Escherichia coli*, *Klebsiella pneumoniae*, *Mycobacterium leprae*, *Shigella dysentariae* and *Salmonella* species, including *S. typhi* and *S. typhimurium*, *Serratia* species and *Staphylococcus aureus*. Eggs of the nematode *Enterobius vermicularis*, which is an extremely common worm in humans, can also be carried by cockroaches.

There is little doubt that cockroaches contribute to the spread of several infections, mainly intestinal ones. Sometimes they may possibly be more important as mechanical vectors than house flies. However, it remains difficult to assess their real importance as vectors because many of the pathogens which cockroaches carry can be transmitted in many other ways. However, in 1956–1962 on a housing estate in California, USA, about 95% of the houses had cockroaches, mainly *Blattella germanica*, and after effective pest control the numbers greatly decreased. But when in 1963 insecticidal treatments ceased (because people complained about the control process), cockroach populations increased dramatically, as did the incidence of hepatitis. Vector control resumed the following year, and both cockroach numbers and cases of hepatitis again decreased significantly. This suggests that cockroaches do spread at least some pathogens.

15.4 Control

Ensuring that neither food nor dirty kitchen utensils are left out overnight will help reduce the number of cockroaches, but if they are present in nearby houses, good hygiene in itself will not prevent them from entering houses.

Sites such as cupboards, wardrobes, kitchen furniture, underneath sinks, stoves, refrigerators and dustbins can be sprayed with insecticides, but resistance can be a problem. Cockroaches have been found resistant to organochlorines, organophosphates, carbamates and pyrethroids, and resistance to all these groups is known in *Blattella germanica*. However, in the absence of resistance, sprays or dusts of the carbamate insecticide

bendiocarb and organophosphates such as malathion and diazinon can be used to control cockroaches. Pyrethroids, including permethrin and deltamethrin, applied as sprays can produce spectacular results in both ***flushing out*** and killing cockroaches. Sprays or aerosols of insect growth regulators (IGRs) such as hydroprene, fenoxycarb or pyriproxfen, sometimes mixed with pyrethroids, can give a reasonably degree of control. The relatively new insecticide chlorfenapyr, which as yet has not been widely used, has also given good control of cockroaches. However, the IGR noviflumuron provides better control, causing as much as a 90% reduction in *B. germanica* numbers. Spraying should be repeated after about a month, and again when cockroaches begin to reappear.

The residual action of sprays on painted and shiny surfaces may last only about 1–4 weeks, but they may be effective for several months on more porous surfaces. However, microencapsulated formulations have a longer residual life and are applied at lower dosages. The residual action of insecticidal dusts is less affected by the type of surface, but dusting is unsightly and so householders may object to it, and dusts should not be used in kitchens in case they contaminate food.

Commercial lacquers and varnishes containing residual insecticides such as diazinon, permethrin or cypermethrin when painted on walls and other surfaces remain effective in killing cockroaches for several months.

Boric acid powder (borax) still remains a very safe and useful chemical, acting both as a contact insecticide and as a stomach poison.

Good control can be achieved when dinotefuran or imidacloprid (nicotinoids) or sulfluramid (sulfonamide) are added to baits, such as peanut butter, dog food and maltose, to which glycerol may be added to increase their attractiveness. Such poisonous baits are best placed in areas having large numbers of cockroaches. Alternatively cockroach pheromones can be placed in simple cardboard or sticky traps to entice cockroaches into them, after which they are either killed or prevented from escaping. However, baits by themselves will not eliminate all cockroaches.

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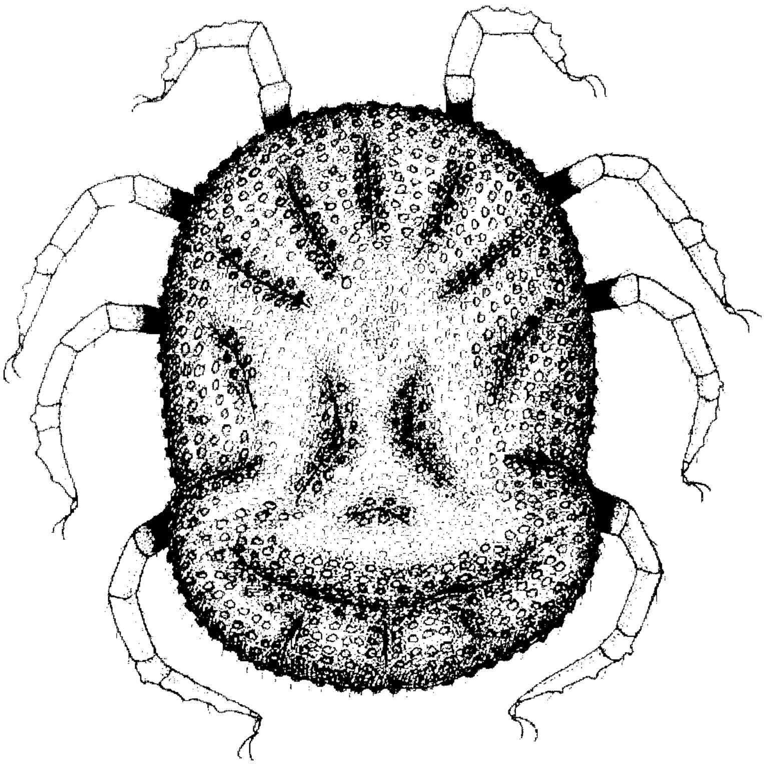
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16

Soft ticks (Argasidae)



Ticks are not insects, because adults have eight legs, not six as in adult insects. They are closely related to mites and spiders. Ticks are divided into two main families, the Argasidae (soft ticks) and the Ixodidae (hard ticks). A third family, Nuttalliellidae, contains just one species which is of no medical importance. Students sometimes find difficulty in distinguishing the very small immature stages of ticks from mites, but ticks differ from mites in having a ***toothed*** hypostome (Fig. 16.2), while adult ticks are also much ***larger*** than mites.

Soft ticks (Argasidae) have an almost worldwide distribution. There are 193 species formerly placed in four genera, but some authorities recognize more genera. The medically important soft ticks belong to the genus *Ornithodoros*. Species in this genus are found in many areas of the world including the Americas, Africa, Europe and Asia. The most important species is *Ornithodoros moubata*, a species in the *O. moubata* species complex, which is a vector of tick-borne (endemic) relapsing fever (*Borrelia duttonii*). A few other species in the *O. moubata* species complex are also of medical importance.

16.1 External morphology

Adult argasid ticks are ***flattened*** dorsoventrally, 8–13 mm long and usually roundish to oval in outline. The integument is wrinkled and usually covered with fine tubercles (mammillae) or granulations. There is ***no scutum*** (dorsal shield) as is found in ixodid (hard) ticks (Fig. 16.1a, Plate 27). The mouthparts, termed the ***capitulum***, gnathosoma, or 'false head', are situated ventrally (Fig. 16.1b) and are ***not visible*** dorsally in the nymphs and adults. This one character separates adults and nymphal soft ticks from hard ticks (Ixodidae), but the larvae of ***both*** soft and hard ticks have the capitulum projecting forwardly and clearly visible dorsally. The four-

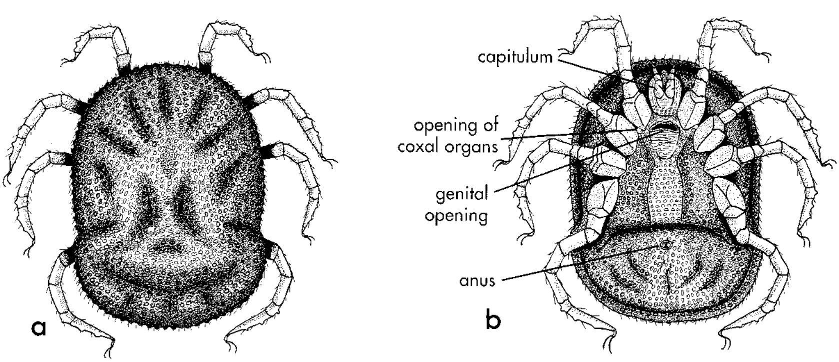


Figure 16.1 Adults of the soft tick *Ornithodoros moubata*: (a) dorsal view; (b) ventral view.

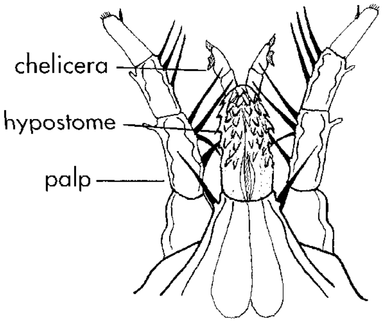


Figure 16.2 Capitulum of an adult *Ornithodoros species, showing leg-like palps and non-denticulate cheliceral sheaths*.

segmented ***palps*** are leg-like, and the powerful cutting chelicerae have smooth, not denticulate, sheaths, and have teeth at their tips (Fig. 16.2). Both the ***chelicerae*** and the ***hypostome*** (Fig. 16.2), which has teeth arranged in several longitudinal rows, penetrate the host during feeding.

The four pairs of legs terminate in a pair of claws. ***Coxal organs*** ('glands') open between the bases of the coxae of the first and second pairs of legs (Fig. 16.1b), and are osmoregulatory in function.

Males and females look very similar and are usually difficult to separate, although blood-engorged females can be considerably larger than males because they ingest much more blood. However, because ***both sexes*** feed on blood and can consequently be disease vectors, it is not usually important to distinguish between them.

16.2 Internal anatomy

A brief account of the internal anatomy of a tick is necessary to understand the mechanisms of disease transmission.

During feeding, saliva, which usually contains powerful anticoagulants, is secreted by a pair of large grape-like salivary glands and flows down the mouthparts into the host. The host's blood passes through the mouthparts and narrow oesophagus into the stomach (mid-gut), which has numerous branching diverticula. Side branches of the diverticula enable the adult tick to ingest large volumes of blood (about 6–12 times its own weight), causing great distension of the tick's body.

Argasid ticks have a pair of ***coxal organs***, which although sometimes called coxal glands are not glandular but filter excess fluid and salts from ingested blood-meals. This fluid passes out through small openings located between the bases of the first two pairs of legs. When a soft tick is infected with tick-borne relapsing fever (*Borrelia duttonii*) many of the spirochaetes in the haemolymph enter the coxal organs and are passed out through their openings. For disease implications, see page 231.

Coxal organs are present only in soft ticks, not in hard ticks.

Females of both soft and hard ticks have a peculiar structure called ***Gene's organ*** located in front of the mid-gut. During oviposition it is extruded from a small opening above the capitulum and secretes waxy waterproofing substances over the eggs, enabling them to withstand desiccation, immersion in water and other adverse environmental conditions.

16.3 Life cycle

A blood-meal is essential for egg production, and in argasids feeding is mainly nocturnal. Female ticks ingest large blood-meals, often increasing their weight 12-fold after feeding, while hard ticks ingest even more blood (see Chapter 17, page 240). After each blood-meal female argasid ticks lay ***several*** (often 4–6) small egg batches, each comprising 15–100 spherical eggs. Occasionally an egg batch has as many as 300–500 eggs. Adult ticks can live for many years, and females may lay thousands of eggs during their lifetime. Eggs are deposited in or near the resting places of adult ticks, such as in cracks and crevices in the walls, floors and furniture of houses, in mud, dust and debris, in rodent holes or in the more exposed resting or sleeping places of wild animals and birds.

Eggs usually hatch after 1–3 weeks, but because they have been coated during oviposition with a protective waxy secretion from Gene's organ (see above) they can remain viable for many months under adverse climatic conditions.

Both argasid and ixodid ticks have a ***hemimetabolous*** life cycle. The eggs hatch to produce six-legged ***larvae*** which superficially resemble the adults, and which moult to produce eight-legged ***nymphs***, which resemble the adults even more closely. In the six-legged larva the capitulum projects from the body and is visible from above (Fig. 16.3). In argasid ticks the larva is usually very active and searches for a host. Blood-feeding may last 20–30 minutes, but in some species for several days, after which the engorged larva drops to the ground and after a few days moults to produce an eight-legged nymph. The nymph seeks a host and feeds for about 20–35 minutes before it falls to the ground. Argasid ticks usually have ***four or five*** nymphal instars (Fig. 16.4), but up to seven in some species. Each nymphal instar requires a blood-meal before it can proceed to the next stage. ***Adults*** usually feed on hosts for 20–35 minutes.

Larvae of *Ornithodoros moubata* differ from most other argasid ticks because they ***do not*** take blood-meals but remain within their eggshells after hatching, and then moult to produce first-instar nymphs, which crawl from the eggshells to seek blood-meals.

The duration of the ***life cycle***, from egg hatching to adult, depends on the species of tick, temperature and availability of blood-meals, but in argasids

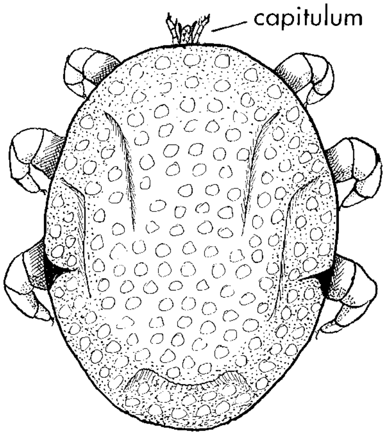


Figure 16.3 Larva of an *Ornithodoros* species, an example of a typical soft tick, showing the capitulum projecting in front of the body and the six legs.

it is typically about 6–12 months. Adult ticks can ***live*** for many years, up to 12–20 years in the laboratory; the record for a tick is 25 years! In the absence of suitable hosts adults can survive up to 10 years without a blood-meal. In argasid ticks mating usually occurs away from the host, such as on the ground or amongst vegetation.

The distribution of the larvae, nymphs and adults of argasid ticks is usually patchy and restricted to the homes of their hosts. Such ticks are called ***nidicolous***, as opposed to the non-nidicolous ixodid ticks, which move further from the homes of the hosts. Species which commonly feed on people, such as *O. moubata* in Africa (the African tampan tick), are found around human settlements, especially in village houses. They can also be found in livestock shelters, chicken sheds, animal burrows, and especially in dry areas in caves. However, in much of Africa argasid ticks appear to be becoming uncommon. This is probably because of changes in lifestyle, such as the increased numbers of people sleeping on beds raised from the floor, which reduces the chance of ticks feeding on them.

Because all nymphal instars and adults take blood, but remain attached for only relatively short periods, many hosts, comprising different individuals and often different species, are fed upon during the life cycle of each tick. Argasid ticks are consequently referred to as '***many-host***', or 'multi-host', ticks.

See Table 16.1 for a summary of the differences between hard and soft ticks.

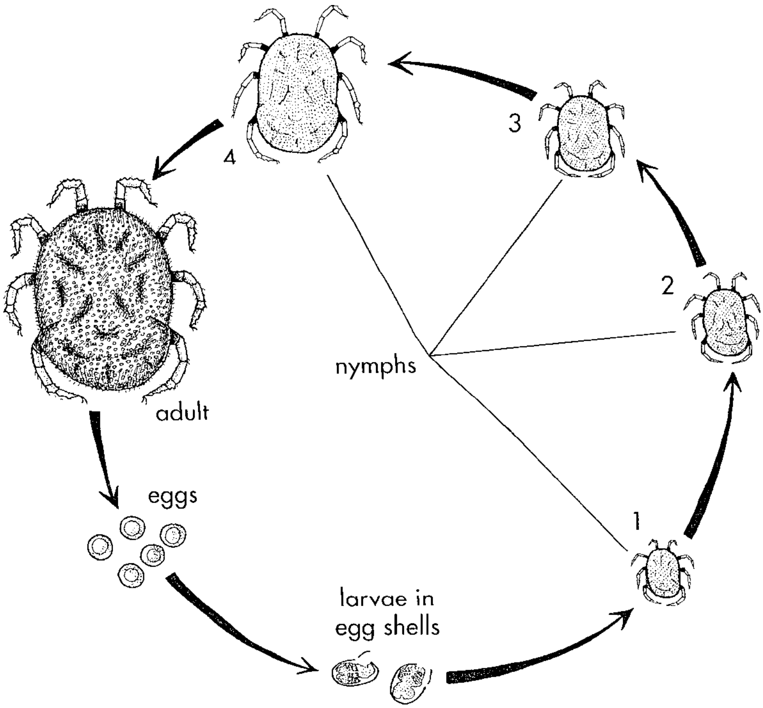


Figure 16.4 Life cycle of *Ornithodoros moubata*, showing larvae retained in eggshells and four nymphal stages.

16.4 Medical importance

16.4.1 Tick-borne relapsing fever

Tick-borne relapsing fever is the only important disease transmitted to humans by soft ticks. The infection occurs throughout most of the tropics and subtropics, and in many temperate areas such as North America and Europe, but is absent from Australia and New Zealand.

There are 15 or more species of *Borrelia*, mostly having different geographical distributions, that cause *Ornithodoros*-transmitted relapsing fevers. The most common is *B. duttonii*, found in sub-Saharan Africa and transmitted by *O. moubata*. In other geographical areas different ticks in the *O. moubata* species complex transmit different species of *Borrelia*.

Spirochaetes ingested with a blood-meal multiply in the mid-gut, penetrate its wall and pass into the haemocoel, where they can be found after 24 hours. In the ***haemocoel***, the spirochaetes multiply enormously and invade nearly all tissues and organs of the tick's body. After three days they infect the ***salivary glands***, the ***coxal organs*** and ***ovaries***.

Table 16.1 *Summary of principal features distinguishing soft and hard ticks*

Argasid ticks (soft ticks)	Ixodid ticks (hard ticks)
Morphology	
Scutum (shield) absent	Scutum (shield) on larvae, nymphs and adults. Females with small, and males with large scutums
Mouthparts (capitulum) not visible dorsally in nymphs and adults, but seen in larvae	Mouthparts (capitulum) visible dorsally in larvae, nymphs and adults
Palps leg-like; chelicerae have smooth sheaths	Palps club-shaped; chelicerae have denticulate sheaths
Coxal organs present	Coxal organs absent
Life cycle	
Eggs laid in several small batches of 15–100 eggs	Eggs laid in one large batch of many thousands of eggs
4–5 nymphal stages (8-legged)	Only one nymphal stage (8-legged)
Adults blood-feed rapidly, on hosts for only 20–35 minutes, but feed on several separate occasions	Adults feed slowly, on hosts for 1–4 weeks, but females feed only once
Multi-host ticks, usually about 6 hosts	Usually 2- or 3-host ticks
Ticks found mainly in or around homes of host, disperse little	Ticks attach to host for long time, hence can disperse considerable distances
Diseases	
Vectors of tick-borne relapsing fever	Vectors of tick-borne typhuses, Lyme disease and many viruses. Cause tick paralysis

In the nymphs of *O. moubata* the salivary glands are more heavily infected than those of the adults. The coxal organs of nymphs are usually only lightly infected, whereas those of the adults become heavily infected. When either nymphs or adults of *O. moubata* blood-feed saliva is injected into the bite, and spirochaetes can be introduced by this route, especially by the nymphs. During feeding, excess body fluids are filtered from the haemocoel by the coxal organs and in infected ticks, especially adults, the coxal fluids contain spirochaetes ingested with a previous blood-meal. These spirochaetes can enter the host through the puncture of the tick's bite or through intact skin. Humans can therefore become infected with *B. duttonii* by either the bite of *O. moubata* or the coxal fluids, or both.

In other *Ornithodoros* species the coxal organs tend to excrete excess fluids only when the ticks have left their host, and consequently transmission by these species is mainly by the tick's bite. In no species of *Ornithodoros* is infection spread by faeces.

The ***tick*** is usually regarded as the most important reservoir host, especially as there is ***transovarial*** transmission. That is, ovaries of adult female ticks become infected with spirochaetes which are then passed to the eggs, so that the newly hatched larvae and all nymphal instars and adults, of both sexes, are infected. So, although nymphs and adults may not have fed on an infected person they can nevertheless transmit *B. duttonii* to other people. Such transovarial transmission can be continued for about three to four generations.

There may also be ***transstadial*** transmission. For example, a larva might become infected by feeding on an infected host and pass the spirochaetes to the nymphs and adults, or the infection might start with a nymph and be passed to subsequent nymphal instars and the adults. In all cases transovarial transmission can follow.

Although *B. duttonii*-transmitted relapsing fever has not usually been regarded as a zoonosis, it seems that in central Tanzania it can be a zoonosis involving chickens and pigs. Some other tick-borne relapsing fevers, such as *Borrelia hermsii* transmitted by the tick *O. hermsi* in the Americas, are also zoonoses, usually having rodents or birds as reservoir hosts.

16.4.2 Q fever

Although Q fever is transmitted mainly by ixodid ticks, argasid ticks can also be vectors. See Chapter 17 (page 247), for an account.

16.4.3 Viruses

More than 100 arboviruses are transmitted by ticks, but only about 30 have been isolated from soft ticks, and very few infect people. Although soft ticks are not regarded as important vectors of arboviruses to humans, a new *Flavivirus* causing Alkhurma haemorrhagic fever has been recorded from Saudi Arabia and Egypt. The principal hosts are camels and other domestic animals; human cases are rare and occur mostly in butchers who have become infected through wounds. *Ornithodoros savignyi* appears to be a vector, as do *Ixodes* species.

16.4.4 Tick-bite allergies and tick paralysis

Several species of ticks can cause allergies such as itching, skin rashes, fevers, vomiting and diarrhoea, including *Ornithodoros* species such as *O. moubata*, but these symptoms are more commonly associated with ixodid ticks (see Chapter 17, page 243).

16.5 Control

Methods used for removing ticks from their hosts are described in Chapter 17 (page 249).

Suitable repellents that can be applied to the skin include DEET, picaridin-based products, dibutyl phthalate or indalone. However, these repellents, especially DEET, are less effective against ticks than against biting insects. Alternatively clothing can be impregnated with permethrin.

Houses infested with argasid ticks, such as *Ornithodoros* species, can be sprayed with insecticides such as the carbonates carbaryl and propoxur, organophosphates such as malathion, or pyrethroids such as deltamethrin or cypermethrin. Floors, cracks and crevices in walls and furniture, and other sites where ticks may be hiding, should be sprayed. In houses where walls are uniformly plastered this usually reduces the numbers of ticks resting in them. When houses have been sprayed with residual insecticides for malaria control there is often a reduction in the numbers of *Ornithodoros* ticks.

When applied to ticks or mites, insecticides are often called acaricides.

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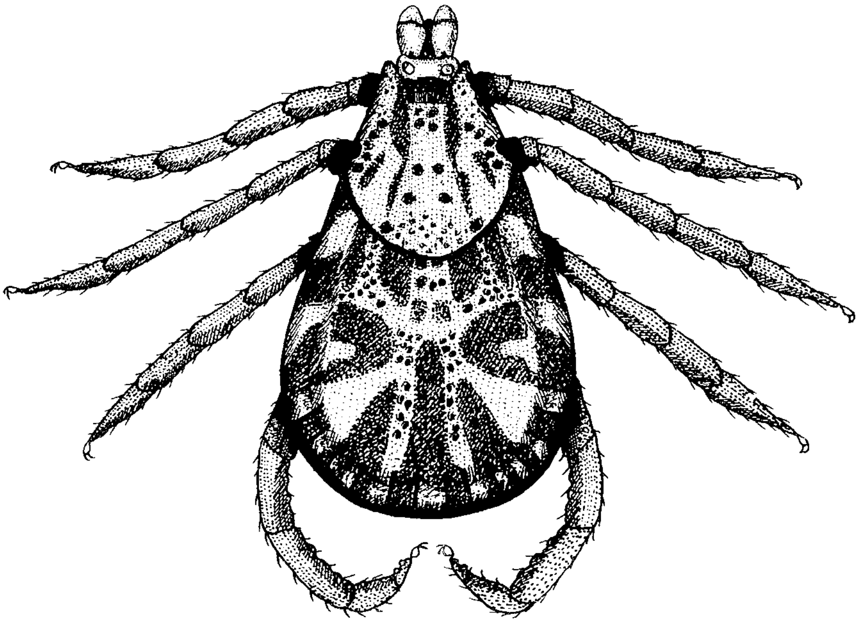
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See also references to hard ticks at the end of Chapter 17.

17

Hard ticks (Ixodidae)



Hard ticks (Ixodidae) have a worldwide distribution, but are more common in temperate regions than soft ticks (Argasidae). There are 702 species of hard ticks belonging to 14 genera. Medically the more important genera are *Ixodes*, *Dermacentor*, *Amblyomma*, *Haemaphysalis*, *Rhipicephalus* and *Hyalomma*. Hard ticks are vectors of typhuses such as Rocky Mountain spotted fever (*Rickettsia rickettsii*) and Meditteranean spotted fever (*R. conorii*), and Q fever (*Coxiella burnetii*). Many arboviruses, including tick-borne encephalitis, Omsk haemorrhagic fever, Kyasanur Forest disease, Crimean–Congo haemorrhagic fever and Colorado tick fever, are transmitted by hard ticks. They also transmit tularaemia (*Francisella tularensis*), and cause tick paralysis.

17.1 External morphology

Adult hard ticks are ***flattened*** dorsoventrally, oval in shape and about 2–23 mm long, size depending on species and whether they are unfed or fully engorged with blood. Females are usually bigger than males, and because they take larger blood-meals they enlarge much more than males during feeding.

The ***capitulum*** or 'false head' projects forwards from the body and is visible from above (Fig. 17.1, Plates 28, 29, 30), thus distinguishing adult hard (ixodid) ticks from soft (argasid) ticks (see Fig. 16.1). Also, in hard ticks the ***palps*** are swollen and club-shaped (Fig. 17.2) rather than leg-shaped as in soft ticks, and the cheliceral sheaths are covered with very small denticles, unlike those of soft ticks. As in argasid ticks, both the ***hypostome*** and ***chelicerae*** penetrate the host during feeding. In hard, but not soft, ticks a

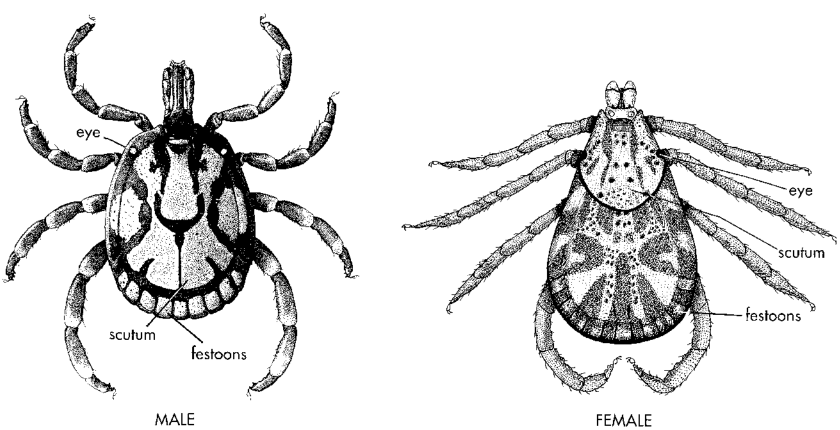


Figure 17.1 Adults of hard ticks: male *Amblyomma* (courtesy of the Natural History Museum, London) and female *Dermacentor*, showing sexual differences. A male ixodid has a large scutum while a female has a small scutum. Note the presence of festoons.

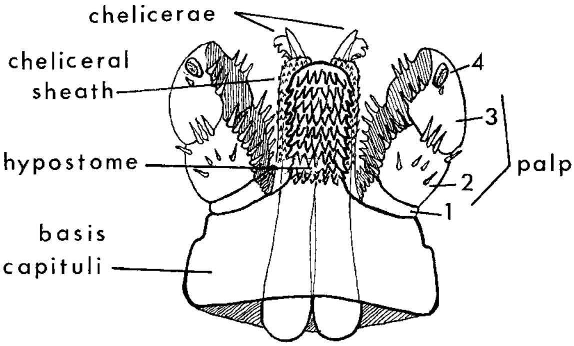


Figure 17.2 Capitulum of an adult ixodid tick, showing club-shaped palps with minute fourth segment, and denticulate cheliceral sheaths.

cement-like substance from the salivary glands 'glues' the mouthparts firmly into the host, and ensures continued attachment during their long feeding times (days to weeks).

The posterior margin of the body in species of *Dermacentor*, *Rhipicephalus* and *Haemaphysalis* has a number of rectangular indentations called ***festoons***. However, in fully engorged females these indentations may be difficult to see because of the body's distension with blood.

Hard ticks have a dorsal plate called the dorsal shield or ***scutum***, which is absent in soft ticks. In ***males*** the scutum is large and covers almost the entire dorsal surface of the body, whereas in ***females*** it is much smaller and restricted to the anterior part of the body (Fig. 17.1). In fully fed females the scutum may be difficult to see because it appears small in relation to the enlarged body and becomes pushed forwards so that it is almost vertical in position. In both sexes of *Dermacentor*, *Amblyomma* and some *Rhipicephalus* species the scutum has so-called enamelled coloured areas, and such ticks are described as ***ornate*** species. The presence of a scutum immediately identifies a hard tick, while a large scutum identifies a male. However, distinguishing the sexes is medically not very important because ***both sexes*** take blood-meals and are therefore potential disease vectors. In the larval and nymphal stages the scutum is small in both sexes.

There are four pairs of legs, with each leg ending in a pair of claws. Coxal organs are absent in hard ticks. The internal organs are basically as encountered in argasid ticks (see Chapter 16, page 228).

17.2 Life cycle

Both ixodid (hard) and argasid (soft) ticks have ***hemimetabolous*** life cycles, that is there is incomplete metamorphosis involving a ***larval*** and ***nymphal*** stage. There are, however, important differences between the life cycles and ecology of hard and soft ticks. ***Adult*** ixodid ticks remain attached to their

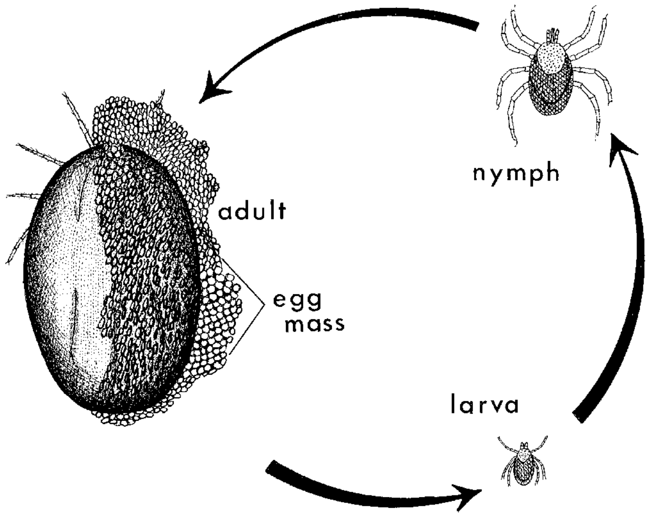


Figure 17.3 Life cycle of an ixodid tick, showing a female with a very large egg mass and a single nymphal stage.

hosts for long periods as blood-feeding often lasts 1–4 weeks. After feeding the enormously engorged tick drops from the host to the ground and shelters under leaves or stones, amongst surface roots of grasses and shrubs, or buries itself in the surface soil. These are termed ***non-nidicolous*** ticks, in contrast to the ***nidicolous*** argasid ticks, which live in hosts' burrows and homes. Time taken for females to digest their blood-meal and commence laying eggs varies according to species and environmental conditions, especially temperature. Sometimes oviposition begins 3–6 days after the female drops from the host, but egg-laying may not begin until several weeks or occasionally months after the end of feeding. ***Thousands*** (1000–10 000) of small spherical eggs are laid in a gelatinous mass which is formed in front and on top of the tick's scutum (Fig. 17.3). A few species lay as many as 20 000 eggs; the largest number recorded was over 34 000 eggs laid by *Amblyomma variegatum*. The egg mass may become larger than the ovipositing female. Oviposition can last 10 days, or extend over a month or more. As in argasid ticks, the eggs are coated with a waxy secretion produced by ***Gene's organ***, which in ixodid ticks also helps transfer eggs from the genital opening to the scutum. The female ixodid tick lays ***only one*** batch of eggs, after which she dies.

After 10–20 days to a few months six-legged larvae hatch from the eggs. The larvae are minute (0.5–1.5 mm long), and are sometimes called ***seed ticks***. On cursory examination they superficially resemble larval mites, but the presence of a ***toothed*** hypostome immediately identifies them as ticks. Newly emerged larvae remain inactive for a few days, after which they

climb up vegetation and wait for passing hosts. When suitable hosts occur they extend their front legs in the air and cling to the hairs or feathers of passing hosts. Such host-seeking behaviour exhibited by the larvae, and also by the nymphs and adults, is called ***questing***. Once on a host the chelicerae and hypostome are inserted deep into the skin and the larva commences blood-feeding. ***Larvae*** remain on their hosts for about 3–7 days before dropping to the ground and sheltering amongst vegetation or under stones. They normally take a few days to digest their blood-meals, but in cooler weather digestion may extend over several weeks. After blood has been digested the larvae remain inactive for a further few days before they moult to become nymphs.

Newly formed eight-legged ***nymphs*** climb up vegetation and behave similarly to the larvae (i.e. ***questing***) in seeking a host. ***Blood-feeding*** lasts 5–10 days, after which fully engorged nymphs drop to the ground and shelter under stones or amongst vegetation. They remain quiescent for a few weeks while the blood-meal is digested, after which the nymphs moult to produce male or female adult ticks. There is only ***one*** nymphal stage in the life cycle of ixodid ticks (Fig. 17.3), whereas argasid ticks have several nymphal stages.

Newly formed adults remain more or less inactive for about a week, after which they climb vegetation and start questing for passing hosts. ***Adult*** female ticks can take enormous blood-meals, ingesting 1–8 ml of blood. Although much of the fluid of this is excreted, the weight of an unfed female can nevertheless increase some 200 times after blood-feeding! In contrast, male ticks ingest much less blood. Adults shelter under stones and surface vegetation, and amongst roots of plants. Except for *Ixodes* species, mating in ixodid ticks occurs on the host, and males may remain on a host for several weeks or months, mating with several females.

17.3 Behaviour and habits

Many species of ixodid ticks are more or less host-specific. For example some species feed almost exclusively on birds, others on reptiles, or on certain types of mammals such as bats, canids or bovids, but other species feed on almost any available hosts, including people. Diversity of host species may increase the likelihood of disease transmission. ***Larvae and nymphs*** of many, but not all, ticks seem to favour feeding on small animals such as rodents, cats and dogs, and ground-inhabiting birds, whereas ***adults*** prefer to feed on cattle, deer, horses and a variety of large and wild mammals. ***Humans*** are mainly parasitized by larvae and nymphs of hard ticks, more rarely by adults.

The ***life cycle*** of ixodid ticks commonly takes 2–4 years, depending on species and availability of hosts, but may be longer due to lack of hosts. In temperate regions development may also be prolonged or cease

temporarily during winter months. In warm countries development and breeding often continue throughout the year; nevertheless there may be seasonal fluctuations in development rates. ***Adult*** ticks usually live for 2–3 years, although some can live up to seven years, and adults may be able to survive 2–3 years of starvation. Although ticks can tolerate considerable variations in temperature and humidity, most species are absent from very dry or very wet areas, although certain *Hyalomma* species occur in arid areas. Microclimatic conditions at soil level are greatly influenced by the amount and type of ground vegetation, and consequently the distribution of tick species is often closely associated with different types of vegetation.

Because immature and adult ixodid ticks remain on hosts much longer than argasid ticks, they may be carried many kilometres by their hosts, or even across continents by migrating birds.

17.3.1 Three-host ticks

The life cycle described above for hard ticks refers to a three-host tick. That is, a different individual host, which may be the same or different species, is parasitized by the larva, the nymph and the adult, and moulting occurs on the ground. About 95% of ixodid ticks have this type of life cycle, and medically important species of three-host ticks are found in the genera *Ixodes*, *Dermacentor*, *Rhipicephalus*, *Haemaphysalis* and *Amblyomma*. Ticks which feed on three hosts are more likely to become infected with pathogens and to be potential vectors than species feeding on just one or two hosts.

17.3.2 Two-host ticks

Larvae of some *Hyalomma* and *Rhipicephalus* species remain on the host after blood-feeding and moult to produce nymphs which feed on the same host. The engorged nymphs then drop off and moult, and the resultant adults feed on a different host. This a two-host tick life cycle.

17.3.3 One-host ticks

In a few ticks, such as *Boophilus* species, the larva, nymph and adult all feed on the same host and moulting also takes places on that host. The only stage that leaves the host is the blood-engorged female tick, which drops to the ground to lay her eggs. One-host ticks are less likely to acquire infections with pathogens than ticks which feed on several hosts, and the only method by which infection can spread from one host to another is by transovarial transmission. One-host ticks are of little or no medical importance, but certain species of *Boophilus* are important vectors of animal infections.

See Table 16.1 (page 232) for a summary of the differences between hard and soft ticks.

17.4 Medical importance

Table 17.1 very briefly summarizes some of the infections transmitted to humans by hard ticks. More details of tick-borne infections are given below under the various headings.

Table 17.1 *Some infections transmitted to humans by hard ticks*

Disease	Infective agent	Principal tick vectors	Main reservoir hosts excluding ticks
Tick-borne encephalitis	*Flavivirus*	*Ixodes ricinus*, *I. persulcatus*	Rodents, insectivores
Omsk haemorrhagic fever	*Flavivirus*	*Dermacentor reticulatus*	Muskrats, water voles
Kyasanur Forest disease	*Flavivirus*	*Haemaphysalis spinigera*, *H. turturis*	Monkeys, shrews, rodents
Crimean–Congo haemorrhagic fever	*Nairovirus*	*Hyalomma marginatum* species complex	Hares, cattle, goats
Colorado tick fever	*Coltivirus*	*Dermacentor andersoni*	Many rodent species, rabbits
Rocky Mountain spotted fever	*Rickettsia rickettsii*	*Dermacentor*, *Amblyomma* and *Rhipicephalus* species	Many rodent species
Mediterranean spotted fever	*Rickettsia conorii*	*Rhipicephalus sanguineus*	Rodents, dogs
African tick-bite fever	*Rickettsia africae*	*Amblyomma* species	Rodents, possibly cattle
Q fever	*Coxiella burnetii*	Many ixodid species	Sheep, goats, cattle, possibly rodents
Human ehrlichiosis	*Ehrlichia chaffeensis*	*Amblyomma* and *Ixodes* species	Deer, rodents
Lyme disease	*Borrelia burgdorferi*	*Ixodes ricinus*, *I. scapularis*, *I. pacificus*	Birds, rodents
Tularaemia	*Francisella tularensis*	Many ixodid species	Rabbits, hares, deer, beavers
Tick paralysis	Tick toxins	Mainly *Ixodes* and *Dermacentor* species	Not applicable, as not caused by any pathogen

17.4.1 Tick paralysis and allergies

Female hard ticks, mainly *Dermacentor* and *Ixodes* species, can cause tick paralysis. Human cases have been reported from North and South America, Europe, Asia, Australia and South Africa. The condition also affects pets and domesticated animals. Symptoms appear 4–7 days after a tick, usually a female, has commenced feeding. There is an acute ascending paralysis affecting firstly the legs, resulting in the patient being unable walk or stand, and later the arms cannot be moved and there follows difficulty in speaking, swallowing and breathing. Symptoms are painless and there is rarely any rise in the patient's temperature. Tick paralysis can be confused with paralysis due to poliomyelitis and certain other paralytic infections. Young children, especially those up to two years, are most severely affected. Death in animals, and in rare cases humans, can result from respiratory failure. Removal of ticks can result in complete recovery after 48 hours, but in severe cases recovery may take a few days, or even up to about six weeks. Only rarely do male ticks cause paralysis, and that is usually in rodents or poultry, not in humans.

Tick paralysis is not caused by pathogens but by toxins in the female tick's saliva which are continually being pumped into the host during the tick's long feeding period. Different species of ticks and also different populations of the same species may vary markedly in their ability to produce tick paralysis in humans and animals.

In some people tick bites can also cause allergies, such as skin rashes, itchy skin, nausea and vomiting, and rarely more serious consequences including death.

Tick paralysis and tick allergies can also occur after bites from argasid (soft) ticks, but this is rare (see Chapter 16, page 233).

17.4.2 Arboviruses

More than 120 arboviruses are transmitted by ticks, but the important tick-borne viral diseases of humans are spread by hard ticks. All arboviruses are transmitted by the tick's bite, and ***transovarial*** transmission usually occurs.

Tick-borne encephalitis (TBE) (*Flavivirus*)

There are three subtypes of TBE, the first of which was described in 1932 as Russian spring–summer encephalitis (RSSE), the second in 1937 was known as central European encephalitis (CEE), then in the early 1980s the Siberian subtype was recognized. All three subtypes are now known collectively as tick-borne encephalitis (TBE), which is widespread in Europe (except the UK, Benelux countries and the Iberian peninsula), Russia, Siberia, Turkey, northern Asia, China and Japan.

In Russia eastwards the main vector is *Ixodes persulcatus*, and in Russia alone there are an estimated 20 000 or more autonomous foci. In Europe *I. ricinus* (Plate 30) is the main vector. Despite having effective vaccines, TBE in Europe increased four-fold between 1974 and 2003. After multiplication in the tick, virus accumulates in the salivary glands, and infection is through the tick's bite. Small rodents such as bank voles (*Myodes glareolus*) and field mice (e.g. *Apodemus* species) are, in addition to ticks, ***reservoir hosts***. There is both ***transstadial*** and ***transovarial*** transmission. Humans are not part of the natural transmission cycle but become accidentally infested with ticks.

TBE virus accumulates in the mammary glands of goats, sheep and cows, and people may become infected by drinking infected unpasteurized milk or eating infected cheese.

Omsk haemorrhagic fever (OHF) (*Flavivirus*)

The virus causing OHF is antigenically very similar to viruses causing TBE and Kyasanur Forest disease (KFD), and clinical symptoms are rather similar to those caused by these other viruses. OHF occurs in Siberia, such as in the Omsk region. The primary vector is *Dermacentor reticulatus* (formerly called *D. pictus*), which feeds on rodents, especially the water vole (*Arvicola terrestris*) and muskrats (*Ondatra zibethida*) which are ***amplifying hosts***, as probably are water voles. Other important vectors are *D. marginatus* and *Ixodes persulcatus*. Infections acquired from animal hosts are transmitted ***transstadially*** to nymphs or adults. ***Transovarial*** transmission also occurs. Muskrat hunters are particularly liable to come into contact with infected ticks, and the disease can also be passed directly to them by the animals' urine and faeces. Infection can also be through drinking milk of goats or sheep.

Kyasanur Forest disease (KFD) (*Flavivirus*)

KFD was first recognized in 1957 when monkeys were dying in Kyasanur Forest in Karnataka State of southern India and people were also becoming ill and dying. The disease is now found in about 5000 km^2 in and around Kyasanur Forest and is associated with movements of people into forests, cattle grazing at the forest edge and deforestion for food crops, activities which expose people to ticks. In 2002 about 22% of inhabitants on the Andaman and Nicobar Islands were seropositive for KFD, and in Saudi Arabia a closely related virus (Alkhurma) was also reported (see Chapter 16, page 233). The main vectors are species of *Haemaphysalis*, especially *H. spinigera*, which transmits the virus to humans, while *H. turturis* maintains animal transmission.

Larval ticks feed on birds and small forest rodents, whereas the nymphal stages feed mainly on monkeys and humans. ***Monkeys***, rodents and shrews (*Suncus murinus*) seem to be the principal ***amplifying hosts*** and reservoir hosts. Larger mammals such as goats, sheep, deer, bison and cattle brought to the forest edge to graze serve as hosts for adult ticks and help maintain large tick populations, but are not reservoir hosts of viral infection. There is ***transstadial*** and probably ***transovarial*** transmission in the tick vectors. The epidemiology of KFD is particularly interesting because it shows how changes in people's behaviour, such as deforestation and agricultural development, can lead to changing ecology and disease outbreaks in the human population.

Crimean–Congo haemorrhagic fever (CCHF) (*Nairovirus*)

CCHF virus is recorded from many countries in central and eastern Europe, the Balkans, Russia, the Middle East, Pakistan, India, China, Madagascar and in Africa from Mauritania to Ethiopia down to South Africa. After dengue viruses, CCHF virus is one of the most widely distributed arboviruses, with human infections known from about 30 countries and virus isolations obtained from ticks in another 10 countries. The disease is typically enzootic in savanna, steppe and semi-desert areas. Transmission is mainly by *Hyalomma* species, such as *H. marginatum marginatum*, but in Africa *H. marginatum rufipes* is the vector. Larval and nymphal ticks feed on birds and small mammals, while adults feed on larger mammals including humans. Hares, cattle and goats are ***amplyfying hosts*** and likely reservoir hosts. Although ***birds*** are not reservoir hosts they can spread infected ticks around the world; for example some 5 billion birds fly annually from Europe to Africa, and about half return.

Transmission is by tick bite and possibly by crushing infected ticks, or by accidental contamination from infected blood during sheep-shearing. ***Ticks*** are regarded as important reservoirs of infection, especially as they can survive starvation for at least 800 days! There is ***venereal*** transmission, i.e. virus is transmitted from infected male ticks to uninfected females during mating, and then ***transovarial*** transmission from infected females to their progeny, followed by ***transstadial*** transmission.

Colorado tick fever (CTF) (*Coltivirus*)

CTF occurs in the Rocky Mountain states and South Dakota in the USA and in western Canada. The principal vector is *Dermacentor andersoni*. Larvae and nymphs feed on small mammals such as rabbits, ground squirrels (*Citellus* species), chipmunks (*Tamias* species) and woodrats (*Neotoma* species), which together with ticks are the main ***reservoir hosts*** of infection. Adult ticks, and sometimes nymphs, feed on larger mammals, such as deer,

cattle and people. There is ***transstadial*** transmission but no evidence of transovarial transmission. A closely related *Coltivirus* (Eyach virus) has been implicated in human disease in the Czech Republic, France and Germany.

17.4.3 Rickettsiae

Tick-borne typhuses have an almost worldwide distribution and are caused by 22 species of *Rickettsia*. Ticks are usually regarded as the main ***reservoirs*** of infection, although rodents and other mammals may sometimes be reservoir hosts. There is usually ***transovarial*** transmission, and often ***transstadial*** transmission. The more important tick-borne typhuses are described briefly below.

Rocky Mountain spotted fever (RMSF)

RMSF, also known as Mexican spotted fever, São Paulo spotted fever, American tick-borne typhus and by several other local names, occurs throughout most of the USA, and less commonly in Canada, Mexico and Central America as well as Colombia and Brazil. The causative agent is *Rickettsia rickettsii*. The principal vector in western America is *Dermacentor andersoni*, and in eastern USA *D. variabilis*, and recently *Rhipicephalus sanguineus* has been found to be a vector in Arizona. In Canada the vectors are also *D. andersoni* and *D. variabilis*. In South America *Amblyomma cajennense* is the main vector, and this species and *Rhipicephalus sanguineus* are the important vectors in Central America. RMSF is a ***zoonosis***, with ground squirrels (*Citellus* species), chipmunks (*Tamias* species) and other small rodents acting as ***reservoir hosts*** and/or ***amplifying hosts***, although the tick itself is considered the main reservoir of infection, especially as infections can persist in overwintering ticks. Dogs are neither reservoir hosts nor amplifying hosts, but they can transport infected ticks to human habitations, where they may become dislodged and attach to people.

Transmission is normally through the bite of any stage in the life cycle of the tick. An infective tick, however, must remain attached to a host for at least 10 hours before transmission can occur. This is because the rickettsia only become virulent after long host attachment. Consequently, early tick removal may prevent transmission. There is both ***transstadial*** and ***transovarial*** transmission.

Mediterranean spotted fever

Also known as boutonneuse fever, Marseilles fever, South African tick typhus, Kenyan tick typhus, Indian tick typhus and Crimean tick typhus. The infective agent is *Rickettsia conorii*. It occurs in the Mediterranean littoral region, Israel, Portugal, Sicily, eastern Russia, India and North

Africa. In the 1990s it was recorded from Uruguay, but it was later shown that this was a misidentification and the infective agent involved was *R. parkeri*. The principal vector of *R. conorii* is *Rhipicephalus sanguineus*, the dog tick. Transmission is by the tick's bite, and both ***transstadial*** and ***transovarial*** transmission occur. Ticks, various rodents and, in contrast to RMSF, dogs can be ***reservoir hosts***. Infection can also occur if infected ticks are ***crushed*** and the rickettsiae rubbed into abrasions or the eyes.

African tick-bite fever

Initially confused with typhus caused by *Rickettsia conorii*, but in 1992 the causative agent was named *R. africae*. This form of typhus is common throughout most of sub-Saharan Africa, and also occurs in the West Indies. In both regions vectors are *Amblyomma* species. Rodents and possibly cattle are ***reservoir hosts***.

Miscellaneous tick-borne typhuses

These include Siberian tick typhus (*Rickettsia sibirica*), Queensland tick typhus (*R. australis*) and Japanese or Oriental tick typhus (*R. japonica*) as well as unnamed diseases caused by other *Rickettsia* species.

Q fever

Q fever is a rickettsial zoonotic disease caused by *Coxiella burnetii*. It was first diagnosed in livestock handlers in Australia as far back as 1935, but is now known to occur in Europe, Africa, Asia and North America. It is primarily an infection of rodents, other small mammals and domestic livestock. It can be transmitted to people by inhalation of aerosolized rickettsia, by consuming contaminated milk or other dairy products, by contamination with aerosols of tick faeces, which can remain infective for months, and by the bites of ixodid, and to a lesser extent argasid, ticks. Sheep, goats and cattle, and possibly rodents, are ***reservoir hosts***, while ticks are probably important in maintaining infections in wild animals and in transmission to domesticated ones. ***Transovarial*** and ***transstadial*** transmission occurs.

17.4.4 Human ehrlichiosis

Species of *Ehrlichia* and *Anaplasma* infect dogs and deer, and some species are zoonotic and also infect humans. One species, *E. chaffeensis*, causes human granulocytic ehrlichiosis (HGE), while *Anaplasma phagocytophilum* and *E. ewingii* parasitize granulocytes and cause human granulocytic anaplasmosis (HGA). Transmission of all three species is by bites of hard ticks such as *Amblyomma* and *Ixodes* species, while rodents and deer appear to be the main ***reservoir hosts***. ***Transstadial*** transmission occurs, and possibly

also transovarial transmission. Ehrlichiosis is widespread in Europe and the USA, where infections seem to be increasing in prevalence, but a few cases of human ehrlichiosis have also been reported from Venezuela and African counties such as Mali, Burkina Faso and Mozambique.

17.4.5 Spirochaetes

Lyme disease

Lyme disease (also called Lyme borreliosis or erythema migrans) was first recognized in 1975 in the town of Old Lyme, Connecticut, USA. It is caused by the spirochaete *Borrelia burgdorferi*, one of 15 species within the *B. burgdorferi* species complex. Here the parasite will be referred to as *B. burgdorferi*, although in some cases of Lyme disease the infectious agent may be another species, such as *B. afzellii* or *B. spielmanii*.

Lyme disease occurs in at least 27 European countries and also in Asia, China, Japan, the USA, South America, Canada, North Africa, sub-Saharan Africa and Australia. In Europe transmission is by the bite of *Ixodes ricinus* (Plate 30) and in Eurasia by *I. persulcatus*. Lyme disease is the most common vector-borne disease in Europe, the USA and several other countries in the northern hemisphere. In the eastern USA the vector is *Ixodes scapularis* (= *I. dammini*), whereas in western areas *I. pacificus* is the principal vector. There is both ***transstadial*** and ***transovarial*** transmission. In many areas of the world the numbers of cases is increasing: for example, in the USA there were 27 444 reported cases in 2007, but this increased to 29 959 confirmed cases and a further 8509 probable cases in 2009.

At least 40 ixodid species and two argasid species are known vectors. Lyme disease is a ***zoonosis***. More than 100 animal species have been identified as being infected, and many species of rodents, insectivores and birds, such as blackbirds (*Turdus merula*) in Eurasia and the American robin (*Turdus migratorius*) in the USA appear to be the most important ***reservoir hosts***. Birds can transport infective ticks long distances and so aid the spread of Lyme disease. Deer, although supporting large populations of vector ticks, are not reservoir hosts.

The ecology of Lyme disease and reasons for its increased prevalence and the extension of its geographical range are both complex and interesting. One explanation is that in both North America and Europe people are spending more recreational time in rural areas where there can be large infestations of deer ticks. Moreover, people are increasingly building homes near to recently cleared land adjacent to forests, and this increases their exposure to ticks. Greater awareness and more extensive serological testing of people may also be partly responsible for the increased numbers of reported cases.

17.4.6 Tularaemia

Tularaemia is a bacterial disease caused by *Francisella tularensis*, of which there are four subspecies. It occurs throughout the northern hemisphere, including the USA, Europe, Turkey, and parts of Asia, the Middle East, northern Africa and rarely in Australia. It infects mainly rabbits and hares, but also small rodents, beavers and deer, all of which can be ***reservoir hosts***. The infection is spread by a variety of direct contact methods such as handling infected live animals or carcasses, drinking contaminated water, inhalation of infected aerosols such as from handling damp hay, eating raw and uncooked meats, and also by the bites of various hard ticks. In Europe the main vectors are *Ixodes ricinus* and *Dermacentor* species. The tabanid fly *Chrysops discalis* has also been identified as a vector in North America.

It is suspected that tularaemia has been used in biological warfare.

17.5 Control

Personal protection methods include application of repellents, such as used for soft ticks (Chapter 16).

Many methods have been advocated for removal of ticks from their hosts, including coating them with Vaseline (petroleum jelly), medicinal paraffin or nail varnish. But it may be several hours before such ticks withdraw their mouthparts and this is usually unacceptable, especially as ***rapid removal*** of ticks often reduces the chances of disease transmission. With soft (argasid) ticks relatively rapid removal may be achieved by dabbing them with chloroform or some other anaesthetic or spraying them with permethrin. But this method rarely works with hard ticks, because they are attached to their hosts with a type of 'saliva cement' that prevents rapid withdrawal of their mouthparts. The recommended procedure is to grasp the tick as close as possible to the host's skin with blunt forceps and slowly pull the tick out. The mouthparts (capitulum) may remain imbedded in the skin and should be removed if possible, and then an antiseptic applied.

Many species of hard ticks transmit livestock infections, and worldwide regular dipping of sheep and cattle in acaricidal baths, or spraying them with insecticides (acaricides) is widely undertaken. Such intensive use of insecticides has resulted in ticks becoming resistant to many types of insecticides; nevertheless, insecticides are still needed to control medically important ticks. For example, dogs can be treated with sprays containing amitraz, carbaryl, permethrin or fipronil to kill ticks which may otherwise attach to humans. Floors of houses, porches, verandahs and other sites where infested pets sleep should be sprayed with insecticides, as outlined in Chapter 16 (page 234) for control of endophilic soft ticks.

Ticks in gardens, yards and nearby fields can be killed by spraying these areas with carbaryl, propoxur, deltamethrin or cyhalothrin. Although

liquid formulations are mostly used, pellet formulations are best when there is dense vegetation because they more easily penetrate ground cover to reach the microhabitats harbouring ticks; a single application may be effective for 6–8 weeks. ULV (ultra-low-volume) spraying with insecticides reduces dosage rates, but there may be environmental objections to such blanket-type spraying of vegetation.

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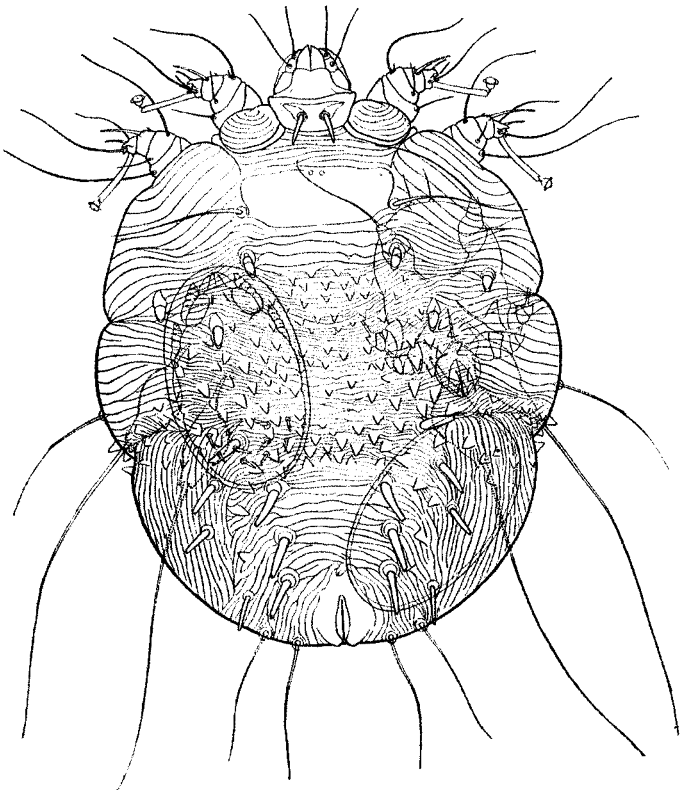
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See also references to soft ticks at the end of Chapter 16.

18

Scabies mites (Sarcoptidae)



Adult mites, like ticks, have eight legs and therefore are not insects. They can be distinguished from ticks by the ***absence*** of teeth on the hypostome of the mouthparts and in having ***setae*** (bristles) on the body as well as the legs. But the principal medically important species (scabies mite, scrub typhus mite, house-dust mite and follicle mite) can most readily be recognized by their characteristic shapes.

Sarcoptes scabiei, the scabies or itch mite, occurs on people worldwide. Morphologically they are indistinguishable from *S. scabiei* infesting wild and domesticated animals, including dogs, horses and pigs. Mites on such animals are considered to be the same species as those infecting people but physiologically adapted for life on non-human hosts. In animals they cause the condition known as mange. Mites living on animals very rarely infect humans, but if they do the infection can persist for several weeks.

Scabies mites are not vectors of any disease but cause conditions known as scabies, acariasis, and crusted or Norwegian scabies.

18.1 External morphology

The female mite (0.30–0.45 mm) is just visible without the aid of a hand lens. It is pale and disc-shaped. Dorsally the mite has numerous tiny ***peg-like spines*** and a few bristles (setae), and both dorsally and ventrally there are wavy lines across the body, giving the mite a striated appearance (Fig. 18.1, Plate 31). Adults have four pairs of short and cylindrical legs divided into five ring-like segments. The first two pairs of legs end in short stalks called ***pedicels*** which terminate in thin-walled roundish structures often termed '***suckers***'. In ***females*** the posterior two pairs of legs do not have 'suckers' but end in long and very conspicuous bristles. There is no distinct head, but the short and fat palps and pincer-like ***chelicerae*** of the mouthparts protrude anteriorly from the body.

Adult male scabies mites are only 0.20–0.25 mm long, and apart from their small size may also be distinguished from females by the presence of '***suckers***' on the last pair of legs (Fig. 18.2).

18.2 Life cycle

Scabies was for a long time associated with poverty, overcrowding and poor hygiene, but people from all socioeconomic backgrounds can become infested with mites.

A virgin ***female mite*** excavates a small pocket in the skin and waits in anticipation of a male entering and mating with her. The fertilized female then digs and eats her way into the surface layers of the skin – the stratum corneum – selecting places where the skin is thin and wrinkled, such as between the fingers and on the wrists, elbows, feet, penis, scrotum, buttocks and axillae. The majority (63%) of mites are found on the hands and wrists, and about 11% on the elbows. In women mites may be found

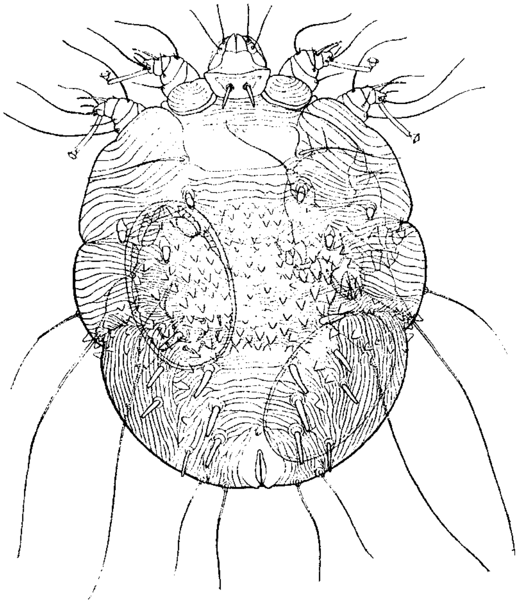


Figure 18.1 Dorsal view of an adult female scabies mite (*Sarcoptes scabiei*). Note the two large oval eggs.

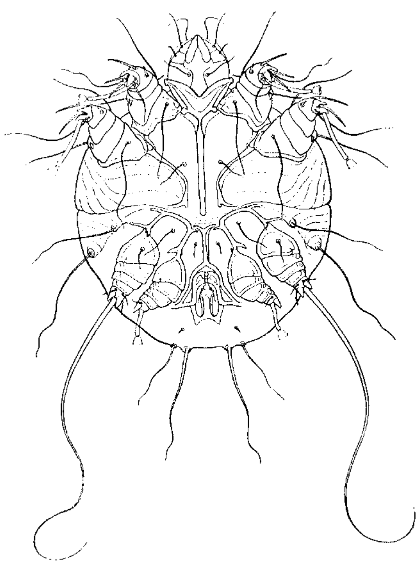


Figure 18.2 Ventral view of the smaller adult male scabies mite, showing 'suckers' on the hind-legs (absent on the hind-legs of females).

burrowing beneath and around the breasts and nipples. Rarely mites are found on the face and scalp, especially in the postauricular fold, and on other parts of the body. The greatest number of mites on children up to a year old are often found on the feet. When females burrow into the skin they excavate winding tunnels at the rate of about 0.5–5 mm per day, which are seen on the skin as very thin twisting lines measuring a few millimetres to 1–2 cm. Mites feed on liquids oozing from dermal cells they have chewed. A female mite lays 1–3 eggs a day in her tunnel.

Eggs hatch after 3–4 days, and small six-legged ***larvae*** emerge which look like miniature adults. They crawl out of the tunnels onto the surface of the skin, where a large number die, but a few succeed in either burrowing into the stratum corneum or entering a hair follicle to produce not a tunnel but a small pocket called a '***moulting pocket***'. After 3–4 days the larva moults in the pocket to produce an eight-legged ***nymph*** (protonymph), which after 2–4 days moults to produce a second nymph (tritonymph). In mites destined to become females this second nymphal stage (tritonymph) is considerably larger than the nymph of a male. After a further 2–3 days the second nymphal stage (tritonymph) moults to become either a male or a female adult. After mating, the female adult increases in size and is sometimes referred to as an ovigerous or mature female. Only after fertilization does the female commence to burrow through the skin, and after 3–5 days begins to lay eggs in her tunnel. Female mites rarely leave their tunnels, but contrary to previous beliefs dislodged healthy female mites can sometimes be found on bed linen and on clothing.

Adult male mites are about half the size of ovigerous females and can be found either in very short burrows (usually less than 1 mm) or in small pockets in the skin. However, they probably spend most of their life wandering around on the surface of the skin searching for unfertilized females in pockets or very short tunnels and eventually mating with a female.

The ***life cycle*** from egg to adult usually takes 10–14 days. Female mites may live for 4–6 weeks on humans, but away from their hosts for only 2–5 days.

Scabies is a contagious complaint which is transmitted only by close contact. It is therefore a family disease spreading amongst those living in close association, especially when they share the same bed. Scabies can be spread between courting couples who are habitually holding hands. It appears that the actual ***transfer*** of mites from person to person takes about 15–20 minutes of close contact. The incidence of scabies often increases during wars and disasters, such as earthquakes, floods and famines, when people are sleeping and living in very overcrowded situations. Although it is possible to become infected by sleeping in a bed formerly occupied by an infected person, this probably rarely happens. As mites may remain alive on towels and discarded clothing for a few days it is possible that some may be able to infest a new host, but such indirect

transmission seems uncommon. Consequently it may not always be necessary to wash or otherwise treat clothing or bedclothes to prevent scabies spreading. However, in epidemics or with cases of ***crusted scabies*** (Norwegian scabies) clothing and bedding should be dry-cleaned or laundered. Ten minutes at 50 °C will kill the mites.

Increases in the incidence of scabies often appear to go in 15- to 20-year cycles, probably due to fluctuations in levels of immunity in the human population, although this explanation has been disputed. It is estimated that global prevalence of scabies is at least 300 million cases annually.

18.3 Recognition of scabies

Scabies can be diagnosed by detection of the female mite's narrow twisting tunnels; faeces deposited in these tunnels may be visible through the skin as dark pepper-like spots. Unfortunately tunnels are not always easy to see, especially on dark-skinned people. However, they can often be made visible by smearing a drop of ink on suspected areas of skin infestations; after a few minutes the ink seeps into the tunnels and when the excess is wiped off they become visible. Alternatively, if liquid tetracycline is used tunnels fluoresce bright yellow-green under ultraviolet light. Surface layers of skin at the ends of the tunnels can be gently scratched away with sharp dissecting needles and the mites, which usually readily adhere to the points of the needles, removed and examined under a ×50 magnification. A cruder procedure is to scrape the affected skin areas with a scalpel blade or razor and to examine the scrapings.

Most people with a healthy immune system have only about 5–15 female mites, children 19–20, and only about 3% have more than 50 mites.

18.3.1 The scabies rash

The scabies rash is a papular eruption that occurs mainly on areas of the body not infected with burrowing mites, such as the buttocks and around the waist and shoulders, but the rash can also occur on other parts of the body such as the arms, calves and ankles. It does not appear on the head, centre of the chest or back, nor on the palms of the hands or soles of the feet. The ***rash*** is in response to an allergic reaction produced by the mites. Frequently patients are unaware they have mites until a rash appears.

When a person is infected for the ***first time*** with mites the rash does not usually appear until 4–6 weeks, although in exceptional cases the rash may occur within 2 weeks. However, in those who have previously been infected a rash may develop within 2–4 days after reinfection. Severe ***pruritus*** soon develops and causes vigorous and constant itching and scratching, especially at night and after hot baths. Scratching frequently causes secondary bacterial infections, which may be quite severe, resulting in boils, pustules, ecthyma, eczema and impetigo contagiosa. Such complications

may hinder the detection of mites, and consequently correct diagnosis of scabies may not be made. The seriousness of the symptoms is not always directly related to the number of mites, and severe reactions may be found on people harbouring few mites. The rash may persist for 2–3 weeks after all scabies mites have been destroyed.

A condition known as ***crusted*** or Norwegian scabies is highly contagious, and although relatively rare it seems to be increasing. It is caused by vast numbers, sometimes many thousands, of mites, and up to 4700 mites per gram of skin have been recorded – which can equate to about 2 million mites on a person! With such a large mite population the skin becomes scaly and hyperkeratotic, and crusts form over the hands and feet and scaling eruptions on other parts of the body, including the head, neck and nails. There is, however, much less pronounced itching. It seems the condition arises due to a loss of immunity, which allows the establishment of enormous numbers of mites. This hypothesis is supported by the development of crusted scabies commonly in patients using corticosteroids, in patients with HIV and in those who are mentally impaired. In such people irritation is reduced and consequently there is less scratching, an act that normally helps in the removal and destruction of mites.

18.4 Treatment of scabies

Permethrin creams are usually the first choice for treating scabies, but there needs to be care with using permethrin on pregnant women and children aged between two months and two years. If permethrin treatment is ineffective then malathion lotions can be used, but care must be taken with children aged six years or younger. These creams and lotions should be applied to the skin from the neck downwards, and when using permethrin washed off after 8–14 hours, but with malathion only after 24 hours. Sometimes a second application a week later is recommended.

When these treatments are unavailable, crotamiton applied as a cream or lotion is a very safe treatment, but 2–5 daily applications are needed. Crotamiton also helps to alleviate itching. If sulphur ointments are used they need to be applied daily for at least a week to be effective; they can also be used on infants and young children. Ivermectin given as a single oral dose or more recently as a topical application is proving effective, but resistance to both permethrin and ivermectin has been documented.

Benzyl benzoate has been used for many years, and may still be appropriate in situations when the above acaricidal creams and lotions are too costly or unavailable locally. An emulsion of benzyl benzoate can be painted on a patient from the neck downwards, and after allowing some 5–10 minutes for this application to dry the patient can re-dress. The emulsion can be washed off after 24 hours. As the one-dose cure rate is only about 50%, a repeat treatment on the third day is usually advisable.

Scabies is highly contagious, so it is important to treat all family members or communities living in close association, such as in nursing homes, not just individuals diagnosed with mites, otherwise reinfections will occur. In such situations, or when there is crusted scabies, it is advisable to launder or dry-clean clothes and bedding to kill any mites on these items.

Killing the mites, however, will do little to immediately alleviate the irritation caused by the rash, and consequently patients will continue to complain of itchiness until the itching eventually disappears. It may therefore be advisable to prescribe antihistamines to relieve any itching.

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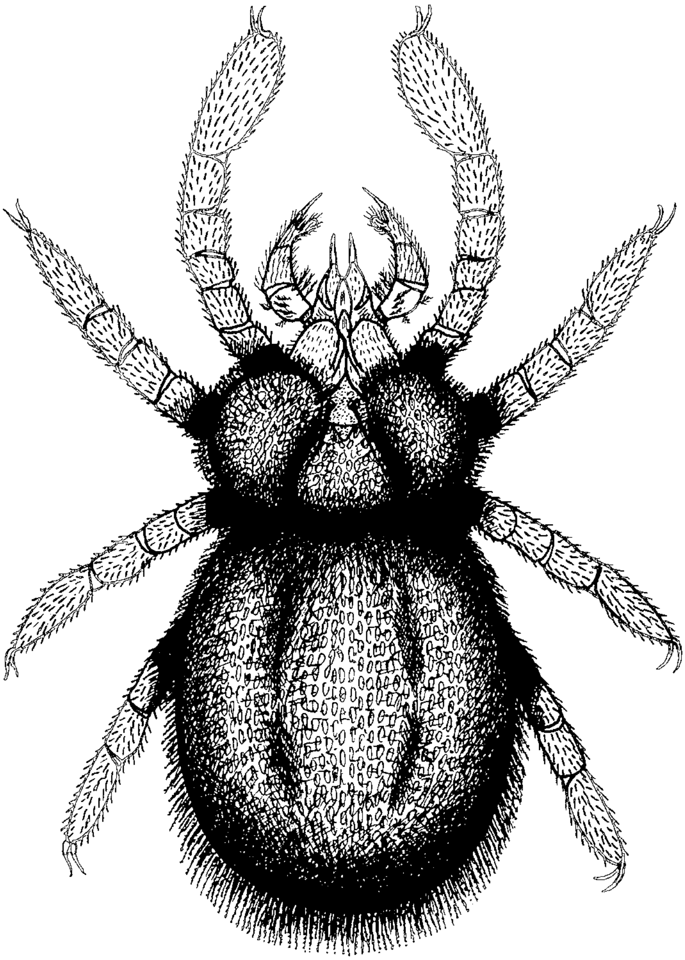
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19

Scrub typhus mites (Trombiculidae)



There are more than 2000 species of trombiculid mites in many genera, but only about 20 species commonly attack people. The family Trombiculidae has a more or less worldwide distribution, but the medically most important species, such as *Leptotrombidium deliense*, *L. akamushi* and *L. fletcheri*, which are vectors of scrub typhus (*Orientia tsutsugamushi*), are found in Asia, the Pacific regions and the northeast coast of Australia.

Other trombiculid mites in many parts of the world cause itching and a form of dermatitis known as scrub itch, autumnal itch or trombidiosis. In northern Europe larvae of *Neotrombicula autumnalis* (***harvest mites***) and in North America and parts of Central and South America larvae of *Eutrombicula alfreddugesi* (***red bugs***) commonly attack people and cause considerable discomfort. Some authors place both these species in the genus *Trombicula*.

19.1 External morphology

19.1.1 Adults and nymphs

Adults are small (1–2 mm), usually reddish, and covered dorsally and ventrally with numerous ***feathered hairs*** giving them a velvety appearance. The four pairs of legs end in paired claws. The body is distinctly constricted between the third and fourth pairs of legs, giving it an outline resembling a ***figure of eight***. Palps and mouthparts project in front of the body and are clearly visible (Fig. 19.1).

Nymphs resemble the adults but are smaller (0.5–1.0 mm) and the body is less densely covered with feathered hairs.

Neither adults nor nymphs are of direct medical importance; they do not bite humans or animals but feed on small arthropods and their eggs. Only the larvae are parasitic and hence disease vectors.

19.1.2 Larvae

Larvae (sometimes known as chiggers) are very small (0.15–0.3 mm) and are just about visible to the unaided eye, but after blood-feeding a larva may increase sixfold in size. Larvae are usually reddish or orange but may be pale yellowish. There are three pairs of legs, with each leg terminating in a pair of relatively large claws. Both legs and body are covered with fine ***feathered hairs***. The five-segmented ***palps*** and ***mouthparts*** are large and conspicuous, giving the larva the appearance of having a false head (Fig. 19.2, Plate 32). Dorsally on the anterior part of the body there is a rectangular or pentagonal ***scutum***, but as it is weakly sclerotized it is often difficult to see under the microscope, unless the light is correctly aligned. More easily detected is a pair of eyes on either side of the scutum. In medically important species there are ***five feathered setae*** on the scutum, and in addition a pair of specialized feathered hairs known as ***sensillae***

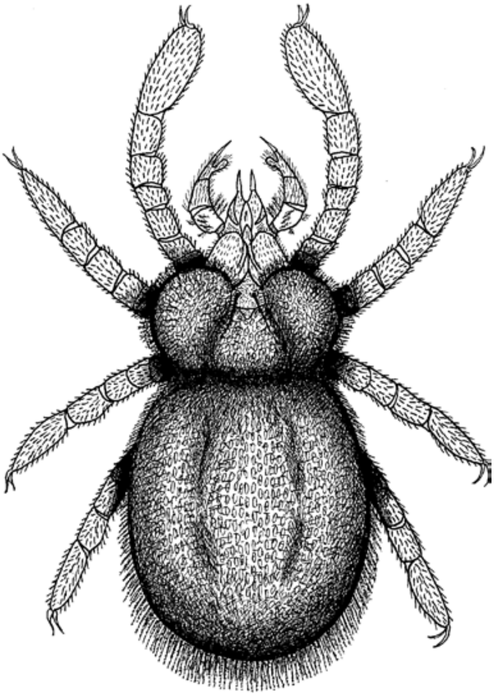


Figure 19.1 Dorsal view of an adult scrub typhus mite (*Leptotrombidium* species).

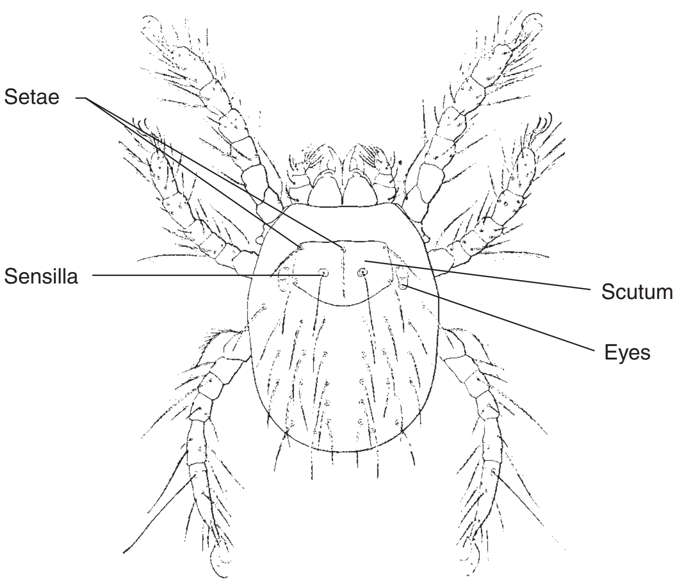


Figure 19.2 Dorsal view of a larval *Leptotrombidium* mite. Note that the scutum has a pair of sensillae and five scutal setae.

which arise from distinct bases. The combination of a body covered with feathered hairs, five scutal hairs, a pair of flagelliform sensillae and large pigmented eyes distinguishes larvae of *Leptotrombidium* from larvae in other mite genera.

19.2 Life cycle

The life cycle of trombiculid mites is complex, and unfortunately several different names have been used for the various larval and nymphal stages (see summarized life cycle on page 264).

Adult trombiculid mites are not parasitic but live in the soil, feeding on a variety of small soil-inhabiting arthropods and their eggs. Females lay 1–5 spherical eggs each day on leaf-litter and the surface of damp but well-drained soil, such as river banks, scrub-jungle, grassy fields and neglected gardens. In hot climates egg-laying continues uninterrupted for a year or more, but in cooler areas of Southeast Asia, as well as in Japan, oviposition ceases during the cooler months and adults enter into partial or complete hibernation.

After about 4–7 days the eggshell splits, but the six-legged larva does not emerge – it remains within the eggshell and is called the ***deutovum*** (Fig. 19.3). After about 5–7 days the larva crawls out of the eggshell and

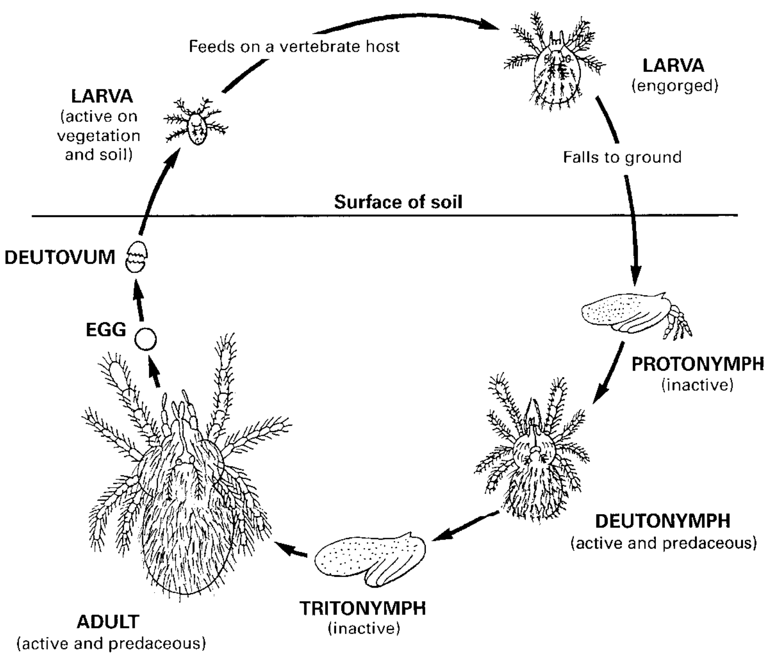


Figure 19.3 Life cycle of a *Leptotrombidium* mite. (Courtesy of the Natural History Museum, London.)

becomes very active, swarming over the ground and climbing up grasses and other low-lying vegetation. Larvae attach themselves to birds and mammals (especially rodents), and also to people walking through infested vegetation. When on a suitable animal host larvae congregate where the skin is soft and moist, such as the ears, genitalia and around the anus. On people larvae seek out areas where clothing is tight against the skin, such as around the waist or ankles.

Larvae pierce the host's skin and inject saliva into the wound which causes disintegration of the cells. Larvae do not suck up blood, but feed on lymph and other fluid and semi-digested tissues. Repeated injection of saliva into the wound produces a skin reaction in the host resulting in the formation of a tube-like structure extending vertically downwards in the host's skin, which is known as the ***stylostome*** or ***histiosiphon***. Some trombiculid mites remain attached to their hosts for up to a month, but the *Leptotrombidium* vectors of scrub typhus remain on people for only about 3–10 days. The engorged larva drops to the ground and buries itself just below the surface of the soil or underneath debris.

Having concealed itself the larva becomes inactive, and this stage is known as the ***protonymph***. After 7–10 days the protonymph moults to produce an eight-legged reddish ***deutonymph*** covered with feathered hairs. These nymphs are not parasitic, but feed on soil-inhabiting arthropods. After a few days to about two weeks the deutonymph ceases feeding, becomes inactive and is called a ***tritonymph***, which after about another 14 days moults to give rise to an adult. Adults resemble nymphs but are larger, and like them are free-living and feed on small soil-inhabiting animals.

The life cycle (Fig. 19.3) usually takes 40–75 days but may be as long as 12 months. The stages in the life cycle can be summarized as follows (the inactive stages are bracketed, and alternative names are in *italics*):

(Egg) → (Deutovum, *prelarva*) → Larva → (Protonymph, *first nymphal stage* or *nymphochrysalis*) → Deutonymph, *second nymphal stage* → (Tritonymph, *third nymphal stage*, *preadult* or *imagochrysalis*) → Adult.

19.3 Ecology

Free-living nymphs and adults need habitats containing sufficient numbers of suitable small arthropods to serve as food, while the larvae require habitats to have small mammals so that they will have hosts on which to feed. ***Rodents*** such as species of *Rattus*, *Apodemus* and *Microtus* and insectivores such as shrews (*Suncus* species) and tree shrews (*Tupaia* species) are important larval hosts. It seems that domestic rats play little or no part in the ecology of scrub typhus. In addition to these hosts other more or less

incidental hosts, including birds, may be important in aiding the dispersal of larvae to other areas.

Areas supporting large populations of mites are frequently formed when people clear away vegetation for agricultural purposes or for the collection of firewood: that is, activities which create ***scrub*** vegetation, from which both the vector and the infection derive their names – scrub typhus. Such habitats favouring colonization by *Leptotrombidium* mites are called '***mite islands***'. These may be very small, often just a few square metres, or they may comprise several square kilometres. This can result in very patchy and isolated distributions of *Leptotrombidium* mites and consequently areas where people are exposed to infection.

19.4 Medical importance

19.4.1 Nuisance

Several species of trombiculid mites attack people in temperate and tropical regions. In northern Europe the main pest is the harvest mite (*Neotrombicula autumnalis*), while in the USA it is the red bug (*Eutrombicula alfreddugesi*). Although these mites do not transmit infections they can nevertheless cause intense itching and irritation, commonly referred to as 'harvest-bug itch', 'autumnal itch' or 'scrub itch'. Larval mites commonly attack the legs. If they are forcibly removed, their mouthparts frequently remain embedded in the skin, and this may promote further irritation. People usually become infested with these mites after walking through long grass or scrub vegetation, especially in the autumn or summer.

19.4.2 Scrub typhus

The causative organism of scrub typhus is the rickettsia *Orientia tsutsugamushi*, and the disease is known as scrub typhus, mite-borne typhus, Japanese river fever, chigger-borne rickettsiosis or tsutsugamushi disease. The disease is restricted to the Asia–Pacific area, extending from the Primorye region of Siberia through Pakistan and India to Myanmar, Indonesia, Malaysia, Thailand, Southeast Asia, China, Taiwan, the Philippines, Japan, Papua New Guinea, New Zealand, northeastern Australia and neighbouring southwest Pacific islands. Although scrub typhus is mostly reported from low-lying areas, it can occur at 1000 m in many areas, and has been reported up to about 2000 m in Taiwan and 3200 m in the Himalayas. During World War II (1939–45) the incidence of scrub typhus in troops in the Asia–Pacific area was second only to that of malaria.

Although more than 40 mite species in 13 genera are known or suspected as being vectors, only about seven species, including *Leptotrombium deliense*, *L. fletcheri*, *L. akamushi* and *L. pallidum*, are important.

People become infected by the bites of larval trombiculid mites when they visit or work in areas having so-called mite islands, that is patches of vegetation harbouring large numbers of host-seeking larvae. The disease is often associated with 'fringe habitats', in other words habitats separating two major vegetation zones such as forests and plantations, because such areas are often heavily populated with rodent hosts. Consequently the risk of scrub typhus transmission is often associated with areas having different types of vegetation (i.e. habitat diversity).

Because each larva attaches itself to only a ***single host*** during its lifetime, scrub typhus cannot be spread by larvae feeding on one infected host (e.g. humans) and then another. Infection acquired by larval mites feeding on hosts infected with *O. tsutsugamushi* is passed on to the free-living nymphal stages and then to the free-living adults. When a female lays eggs they are infected with rickettsiae, and this infection is passed to the emerging larvae. So, although larvae have not previously fed on humans they are already infected and consequently transmit the disease to their hosts (humans or rodents) when they feed for the first and only time. In addition to such ***transovarial*** transmission there is also ***co-feeding*** transmission. That is, when a larva is feeding very near an infected larva which is also feeding, the rickettsiae being injected into the host from the infected larva can be picked up by the nearby previously uninfected larva. This acquired infection can then be passed through subsequent immature stages to adult mites, females of which will lay rickettsia-infected eggs.

Leptotrombidium mites themselves are the main ***reservoirs*** of infection.

19.5 Control

Repellents applied to the skin, such as DEET, dimethyl carbamate or benzyl benzoate, can help reduce the likelihood of people becoming infested with mites. Clothing, especially socks and trousers, can be impregnated or sprayed with repellents or permethrin.

The patchy distribution of chigger mites makes their control very difficult. However, if mite islands are identified then scrub vegetation can sometimes be destroyed mechanically, with herbicides or by burning. This approach is not practical if mites are inhabiting cultivated land where ground vegetation consists mainly of crops. When insecticides (acaricides) such as carbaryl, propoxur, permethrin, deltamethrin or cyhalothrin are sprayed on vegetation harbouring mites they can be substantially reduced in number. Pellet formulations are better when ground cover is extensive. Insecticidal applications can be from ground-based sprayers or from aircraft. Ultra-low-volume (ULV) spraying can also be undertaken. There needs to be care that watercourses and food crops are not also sprayed, and in some situations such blanket insecticidal coverage of vegetation may not be environmentally acceptable.

Control of rodent species that are important larval hosts may sometimes be practical.

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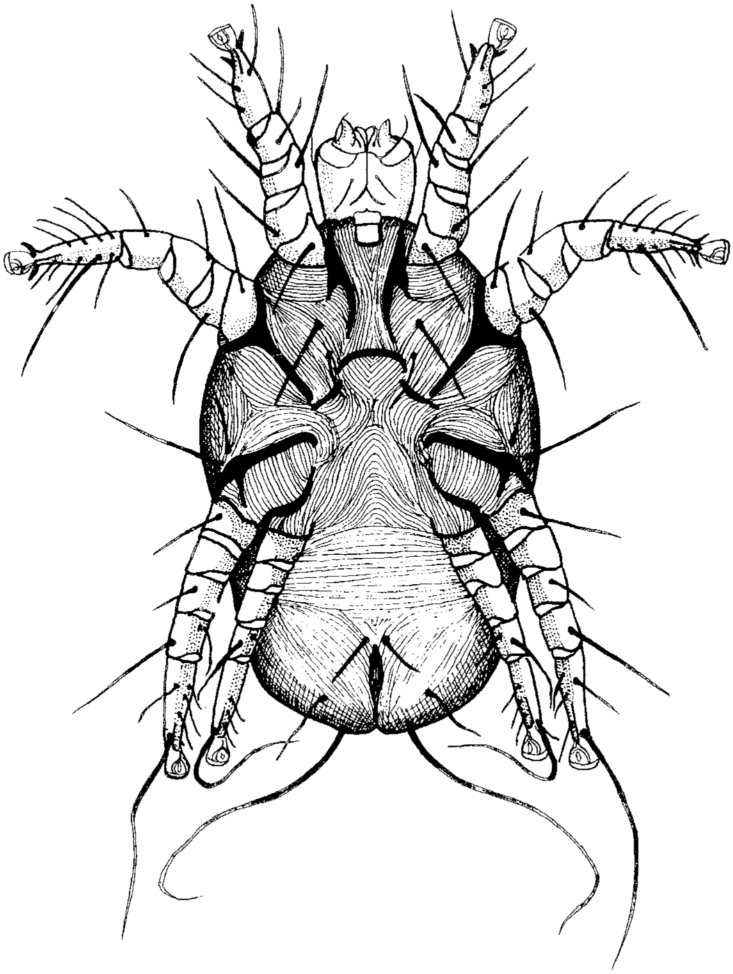
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20

Miscellaneous mites



In addition to scabies mites (Chapter 18) and scrub typhus mites (Chapter 19) there are many other species of mites that can be of medical importance. The most important two, the follicle mites and the house-dust mites, are described below, followed by very brief mentions of a few other mites.

20.1 Demodicidae: follicle mites (*Demodex* species)

Two species of *Demodex* commonly infect humans, namely *Demodex folliculorum* (Fig. 20.1) and *D. brevis*. The former is the more elongate species (0.2–0.4 mm long) and primarily inhabits hair follicles and eyelash hair follicles, whereas *D. brevis* is squatter (0.15–0.2 mm) and lives in the sebaceous glands of hairs and eyelashes. A single follicle may contain 25 *D. folliculorum*, but sebaceous glands contain many fewer *D. brevis*. Both species have a striated body and four pairs of very short stubby legs; they are remarkably non-mite-like. These mites occur only on humans.

Demodex mites feed on subcutaneous tissues, especially sebum, and are particularly common on the forehead, nose, eyelids and cheeks adjacent to the nose. Eggs hatch to produce six-legged ***larvae*** which moult to give rise to ***protonymphs***, then nymphs, and finally adults. All the developmental stages, which extend over 13–15 days, occur within the hair follicles or sebaceous glands. Transfer of mites is believed to occur between mothers and infants during the close contact of nursing. Incidence of infection increases with age, and it seems that 90–100% of older people have these mites!

However, most people are unaware they have mites because they have not produced any adverse effects, and control methods are therefore unnecessary. But occasionally mites cause eruptions on the face such as acne, rosacea, impetigo contagiosa or blepharitis. Repeated daily washing with a diluted baby shampoo or sulphur soaps followed by antibiotic cream may reduce infections, especially around the eyelashes. For more serious cases, zinc and sulphur creams have been used, as have oils of lauric and capric acids, although often with poor results. More recently permethrin cream or sodium sulfacetamide formulations have given better results. In trials oral dosages of ivermectin have shown promise in killing the mites.

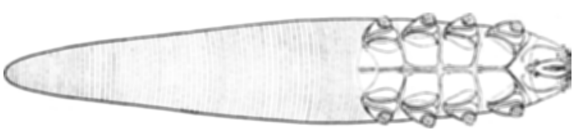


Figure 20.1 Ventral view of hair follicle mite (*Demodex folliculorum*), showing four pairs of stumpy legs.

20.2 Pyroglyphidae: house-dust mites (*Dermatophagoides* and *Euroglyphus* species)

About 20 species of mites are found in house dust. The most common are *Dermatophagoides pteronyssinus*, known as the European house-dust mite, which occurs in North America as well as Europe, and *D. farinae*, the American house-dust mite, which occurs in the USA and central and southern Europe. However, both species are found more or less worldwide. Another house-dust mite, *Euroglyphus maynei*, also has an almost worldwide distribution.

Dermatophagoides (Fig. 20.2) and *Euroglyphus* mites are very small (0.3 mm) and live among bedclothes, mattresses, carpets and general house dust. Female mites lay about 1–3 eggs a day. These hatch after 6–12 days and a six-legged ***larva*** emerges, which feeds and passes through two ***nymphal*** stages (i.e. protonymph and tritonymph) before becoming an adult. The complete life cycle takes about 3–4 weeks. ***Beds*** are the most important, and sometimes only, breeding site. House-dust mites have also been found breeding in clothes such as suits hanging in bedroom wardrobes (closets).

Mites feed on fungi growing on floors and mattresses, discarded skin scales, semen and other organic debris. ***High humidities*** (65–70%)

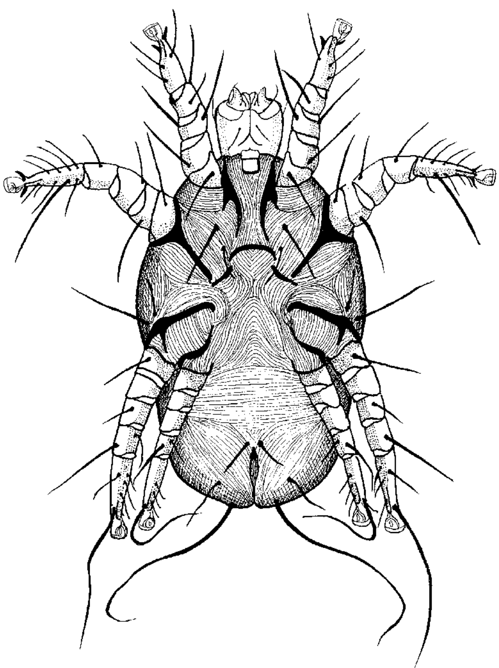


Figure 20.2 Ventral view of a house-dust mite (*Dermatophagoides pteronyssinus*)

are required for mite survival and breeding; however, the protonymph can survive for months at low humidities. Adults live about 1–2 months and produce 40–80 eggs. They are very rarely seen but become airborne when beds are made and are easily inhaled, together with their faeces, and this can cause allergic symptoms resulting in asthma, rhinitis and eczema.

Typically there may be 300 mites per gram of house dust. Under ideal breeding conditions some 5000 mites may be found in just 1 g of mattress dust, but up to 15 600 have been recorded! ***Densities*** above 100 mites per gram are considered a risk factor for sensitization to allergies such as bronchial asthma, rhinitis, conjunctivitis and sometimes atopic eczema, while 500 mites per gram is a major risk factor in the development of acute asthma in those allergic to house-dust mites.

Vacuum-cleaning carpets may have little effect on removing live mites because they cling firmly to carpet fibres, although it may be better in removing mites from mattresses and sheets. However, vacuum-cleaning may increase allergies by creating mite-infested dust storms. Enclosing mattresses and pillows in plastic covers can help reduce mite infestations, although sleeping under such conditions may be uncomfortable. Washing bedding in water above 55 °C or dry-cleaning will kill mites, as will leaving electric blankets switched on at maximum temperature for six hours or more during the day. Treating sheets with benzyl benzoate can be effective in killing mites, as can spraying carpets with permethrin. Insecticide-treated mattress covers have been promoted, but such impregnated items may themselves cause allergies in sensitive people, including those already suffering from mite allergies.

There are several commercial companies that sell insecticidal sprays, and others that claim they can eliminate, or at least greatly reduce, house-dust mite infestations. But it can be very difficult to reduce mite densities sufficiently to result in any reduction in allergies. In fact a meta-analysis has shown that none of the above control measures are effective in significantly reducing asthma or other allergies (Gøtzsche *et al*. 1998).

20.3 Other mites

Numerous other mites are parasitic on mammals and birds, including pets and livestock, and also insects, and some occasionally become parasitic on people. For example, *Pyemotes tritici*, known as the grain mite or hay or straw itch mite, usually parasitizes larvae of grain moths but will bite people handling infested grain or straw. The cosmotropical rat mite (*Ornithonyssus bacoti*), the tropical fowl mite (*O. bursa*) and the chicken mite (*Dermanyssus gallinae*) may sometimes attack people, especially those working closely with infested animals. Bites from these mites can cause irritation and dermatitis. A few species such as *Liponyssoides sanguineus*,

which is normally ectoparasitic on mice and rats, can transmit rickettsial pox (*Rickettsia akari*), and this mite and a few other species can also transmit Q fever (*Coxiella burnetii*) to humans.

There are also other mites, such as forage mites that live among stored products such as grain, copra, flour, dried fruits, cheese and animal feeds. People habitually handling these substances may develop allergic symptoms such as dermatitis, and more rarely bronchitis and asthma. This may lead to terms such as 'grocer's itch', 'baker's itch', and 'copra itch' to describe these occupational hazards.

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Appendix Names of some chemicals and microbials used in vector control (with common trade names in parentheses)

Carbamates
Bendiocarb (Ficam)
Carbaryl (Sevin)
Propoxur (Arprocarb, Baygon)

Formamidines
Amitraz (Mitaban)
Chlordimeform (Fundal, Galecron)

Inorganics
Borax

Insect growth regulators (IGRs)
Cyromazine (Larvadex)
Diflubenzuron (Dimilin)
Fenoxycarb (Insegar, Logic)
Flufenoxuron (Cascade)
Hydroprene (Protrol)
Kinoprene (Enstar)
Lufenuron (Sentinel)
Methoprene (Altosid)
Novaluron (Rimon)
Noviflumuron
Pyriproxyfen (Cyclio, Nylar)
Triflumuron

Microbials
Bacillus sphaericus (Vectolex)
Bacillus thuringiensis var. *israelensis* (*Bti*) (= *Bacillus thuringiensis* H-14) (Aquabac, Teknar, Vectobac)
Spinosad (fermentation of an actinomycete bacterium, *Saccharopolyspora spinosa*)

Monomolecular films
Isostearyl alcohols (Arosurf MSF, Agnique MMF)
Lecithins

Natural organics
Neem oil
Petroleum oils
Pyrethrum

Nicotinoids
Dinotefuran
Imidacloprid

Organochlorines
DDT, i.e. dichlorodiphenyltrichloroethane
Endosulfan
HCH, i.e. hexachlorocyclohexane (formerly BHC)
Lindane
Methoxychlor (Chemform, Methodox)
Toxaphene (Camphechlor)

Organophosphates
Azamethiphos
Bromophos
Chlorpyrifos (Dursban)
Coumaphos (Muscatox)
Diazinon
Dimethoate
Dioxathion (Hercules)
Fenchlorphos (Fenchlorvos, Ronnel)
Fenitrothion (Nuvanol, Sumithion)
Fenthion (Baytex)
Malathion (Carbophosm)
Naled (Dibrom)
Phoxim
Pirimiphos-methyl (Actellic)
Temephos (Abate)
Trichlorton (Dipterex)

Pheromones
Muscalure

Phenylpyrazoles
Fiprinol (Frontline, Top Spot, Termidore)

Pyrethroids
Allethrin (Bioallethrin, Pynamin)
Alpha-cypermethrin
Betacyfluthrin
Bifenthrin (Brigade, Talstar)
Cyfluthrin (Baythroid)
Cyhalothrin (Karate, Kung Fu)
Cypermethrin (Cymbush)
Cyphenothrin (Arrivo, Ripcord)
Deltamethrin (K-Othrin, Decis)
Esfenvalerate
Etofenprox
Fenvalerate (Bhasma, Tribute)
Lambda-cyhalothrin (Icon)
Permethrin (Ambush)
Phenothrin (Sumithrin)
Resmethrin (Bioresmethrin)
Tetramethrin

Pyrroles
Chlorfenapyr (Pirate, Pylon Miticide)

Repellents
Autan (Cutter Advanced) – a picaridin-based compound
Bayrepel (KBR 3023) – a picaridin-based compound
Benzyl benzoate (Ascabiol)
Citronella oil
DEET, i.e. diethyl-3-methylbenzamide (formerly called diethyl-meta-toluamide)
Dibutyl phthalate
Dimethyl carbamate
Lemon eucalyptus oil
PMD – a botanical compound (para-menthane-3,8-diol) derived from lemon eucalyptus

Sulphonamides
Sulfluramid

Synergists
Piperonyl butoxide

Glossary of common terms relevant to medical entomology

This glossary contains terms that are used in this book, and a few others that do not appear in it but which are considered pertinent to vector biology and control. In general morphological names are excluded, as these are adequately explained in the various chapters. As usual with glossaries, the inclusion and exclusion of terms is somewhat subjective.

Acaricide Chemical that kills mites and ticks. Most acaricides are also insecticides.

Aestivation Condition in which an organism has a period of inactivity as an adaptive response to unfavourable conditions encountered during the summer, or in the tropics the hot or dry seasons, e.g. aestivating adults of some *Anopheles* species.

Afrotropical region (formerly Ethiopian zoogeographical region) The countries of Africa south of mid-Sahara, including southern Arabia, Madagascar, Seychelles and Cape Verde Islands. *See* Zoogeographical regions.

Allopatric Species that occur in distinct and different geographical areas, so there can be no breeding between these isolated species. *See* Sympatric.

Amastigote Morphological form of species of *Leishmania* and *Trypanosoma* with a rounded body and without a flagellum that occurs predominantly in macrophages (*Leishmania* species) or muscle cells (*T. cruzi*) of a vertebrate host.

Amplifying host Usually used in relation to arboviruses where a host attains a very high level of parasites in its blood (high viraemic titre) which makes it very infective to vectors. For example, pigs develop high viraemias of Japanese encephalitis and are important amplifying hosts, as are monkeys in the transmission of Kyasanur Forest disease. Often not an efficient host for long-term maintenance of parasite populations.

Anautogenous Refers to females of blood-sucking insects that require at least one blood-meal to develop their eggs. *See* Autogenous.

Anthropophagic (anthropophilic) Refers to blood-sucking arthropods that prefer to feed on humans rather than other hosts. The degree of anthropophagy can vary geographically within species as well as between species. *See* Host preference.

Aperiodic (non-periodic) Not exhibiting periodicity. When applied to microfilariae of helminths it means they are neither periodic nor

subperiodic in their appearance in peripheral vertebrate blood, e.g. *Onchocerca volvulus*.

Arbovirus From *ar*thropod-*bo*rne *virus*. A virus that multiplies in a blood-sucking arthropod and is principally transmitted by the bite of arthropods to vertebrate hosts, e.g. yellow fever virus. Viruses, such as myxoma virus in rabbits, transmitted mechanically by arthropods (e.g. fleas and mosquitoes) and involving no cyclical development in the vector are not arboviruses.

Australasian region Australia, Tasmania, New Zealand, Melanesia, Micronesia and Polynesia. *See* Zoogeographical regions.

Autogenous Refers to females of blood-sucking insects (usually mosquitoes and simuliids) that lay at least the first batch of eggs without a blood-meal. Subsequently a blood-meal is required for each further oviposition. Some mosquitoes, e.g. *Toxorhynchites* species, never blood-feed and are thus always autogenous. *See* Anautogenous.

Biodegradable insecticide Insecticide that does not accumulate in the environment but is broken down by microorganisms in the soil and water into relatively harmless compounds, e.g. the organophosphates and carbamates.

Biological control (biocontrol) Deliberate introduction, or augmentation, of biological agents such as pathogens, parasites and predators (especially fish) to control arthropod populations, mainly mosquito larvae. Although *Bacillus thuringiensis* var. *israelensis* is often included in this category it is not a biological control agent because it does not recycle and persist in the environment but is applied as a non-living formulation and is thus more accurately described as a microbial insecticide.

Biological transmission Transmission of disease organisms with biological involvement between the vector and parasite. Can involve (1) multiplication without change in form, e.g. *Yersinia pestis* in fleas, arboviruses in ticks and mosquitoes; (2) multiplication with change in form, e.g. *Plasmodium* species in *Anopheles*; or (3) no multiplication (usually a decrease in parasite numbers) but with change in form, e.g. filarial parasites in mosquitoes and black flies.

Borrow pit Excavation, often by the side of a road or railway, dug to provide earth for buildings or embankments. These fill with water and become mosquito larval habitats.

Bromeliad An epiphytic plant growing on trees in the Americas. Its water-filled leaf axils are colonized by mosquito larvae. *See* Epiphyte.

Campestral In epidemiology, used to describe transmission occurring in fields and open spaces, such as plague transmission among wild rodents. But also used sometimes to include transmission in woods and forests, which strictly is sylvatic transmission.

Carbamates Synthetic insecticides which are derivatives of carbamic acid, e.g. carbaryl and propoxur.

Chemosterilant Chemical used to induce sterility, but not usually death, in arthropods so as to control them, e.g. apholate and tepa. Chemosterilized insects are sometimes used in genetic control of insect vectors.

Chitin A constituent of arthropod cuticle giving it a hard or leathery texture. Some insect growth regulators (IGRs) prevent chitin formation and are used in the control of vectors.

Co-feeding Sometimes an infection can be passed from an infected vector feeding on a host to a nearby uninfected vector. This phenomenon has been recorded in mosquitoes, ticks and mites, such as in the transmission of scrub typhus.

Commensal Animals living together or in close association, e.g. roof rats (*Rattus rattus*) living in and around human habitations.

Cosmopolitan Occurring worldwide or nearly so. May be applied to a species.

Cryptic species Species within a species complex that appear taxonomically identical but differ in their ecology. Some life-stages of cryptic species can be identified by non-morphological techniques such as by their polytene chromosomes, by DNA probes or by cross-mating experiments.

Cytoform (cytotype) A cytologically defined population with a distinctive chromosomal complement, which may be a species or considered as a chromosomal variant within a species. In the latter case individuals are often given vernacular geographical names, e.g. *Anopheles gambiae* Savanna and Forest forms. Different cytoforms may exhibit differences in behaviour.

Dead-end host Host that although infected with an arbovirus or other pathogen, and maybe severely affected, has a viraemia too low in titre to infect blood-feeding arthropods. Examples are humans in the epidemiology of Japanese encephalitis, and horses in western equine encephalitis transmission.

Definitive host Host in which parasites reach maturity. This rarely occurs in arthropod vectors, but the noted exception is the development of malarial parasites, involving sexual reproduction, in mosquitoes. *See* Intermediate host.

Diapause State of inactivity or arrested development which allows an organism to survive a period of unfavourable conditions. Development cannot be resumed, even under favourable conditions, until diapause is 'broken' by environmental stimuli such as changes in photoperiod (length of daylight) or temperature.

Dichoptic A condition of the head in adult Diptera in which the eyes are widely separated from each other, as, for example, in female adult simuliids. *See* Holoptic.

Diel periodicity Periodicity that occurs about every 24 hours.

Diurnal Refers to activity during the daylight hours, such as blood-feeding in simuliids and appearance in peripheral vertebrate blood of microfilariae of some helminth species, e.g. *Loa loa*.

Ecdysis *See* Exoskeleton.

Emulsion Suspension of minuscule droplets of one liquid in another. For example, when an insecticide dissolved in oil is mixed with water this results in a milky emulsion.

Endemic Describes a disease in a human population that is constantly present and more or less stable. The numbers of new cases cannot exceed the numbers of new susceptible individuals entering the population, but may be fewer. The opposite is epidemic. In animal populations the equivalents are enzootic and epizootic.

Endophagic Describes insects, such as some mosquitoes, that enter houses to blood-feed.

Endophilic Describes insects, such as some mosquitoes, that rest in houses before or after blood-feeding in houses or outside.

Endotoxin Toxin formed inside Gram-negative bacteria that is released only when the bacteria are lysed (broken down). An example is the toxins in the parasporal body of *Bacillus thuringiensis* var. *israelensis*, which on ingestion are lethal to simuliid and mosquito larvae.

Epidemic Occurrence of a disease in the human population where the numbers of cases exceed the normal expected number of cases. An epidemic situation can be only temporary. *See* Endemic.

Epimastigote (crithidial form) Morphological form of a trypanosome with the flagellum emerging about halfway in the body but remaining attached to the cell membrane, e.g. trypanosomes in the salivary glands of tsetse flies and mid-gut of triatomine bugs. This is not the stage that is infective to the vertebrate host. *See* Metacyclic trypanosome.

Epiphyte Plant that grows on other plants, usually trees, but without being parasitic. It derives its water mainly from rain. Bromeliads, the water-filled leaf axils of which provide mosquito larval habitats, are epiphytes.

Eurasia A geographical area comprising the continental land mass of Europe and Asia combined.

Exophagic Term applied to insects that blood-feed outside houses, e.g. *Aedes aegypti* and simuliid species.

Exophilic Term applied to blood-sucking insects that rest outside houses, irrespective of whether they have fed inside or outside houses.

Exoskeleton Outer body layer, often called the integument or cuticle, of arthropods that is shed during moulting from one life-stage to another, e.g. third-instar mosquito larva to fourth-instar, and then fourth-instar larva to pupa.

Extrinsic incubation period Duration of the part of a parasite's life cycle that is completed in a vector; that is, the time from a vector becoming infected to it being infective (i.e. capable of transmitting the parasite).

Exuvia The cast-off skin (exoskeleton) of a larval stage or pupa as an arthropod progresses to the next developmental stage. Often referred to in the plural as exuviae.

Fomite An inanimate object that can become contaminated with infectious organisms which can then be transmitted to other people. For example, bacteria on doorhandles, towels, bedding and clothing.

Formamidines A group of acaricidal compounds sometimes used to kill *Demodex* mites.

Genetic control Special type of biological control that uses genetic techniques to control pest populations. Specifically the reduction of the reproductive potential of vectors. For example, the release of sterilized male vectors into field populations which results in producing large numbers of mated, but infertile, females. These females lay eggs that cannot hatch, so causing a population decrease. *See* Sterile male release.

Gnat Many people use this word to refer to biting insects such as mosquitoes or *Culicoides* midges, but the word gnat is a non-scientific name, although a popular word, that can include non-biting insects which are nevertheless causing a nuisance.

Gonotrophic cycle Time from first blood-feeding to oviposition, and subsequently between successive ovipositions. The first such gonotrophic cycle may be a day or two longer than subsequent ones. Sometimes the gonotrophic cycle is defined as time from blood-feeding to blood-feeding. This cycle is sometimes called the ovarian cycle.

Habitat Usually means the physical environment in which an animal lives, e.g. the skin in the case of scabies mites, streams for simuliid larvae and animal nests for many ixodid ticks.

Haemocoel Main body cavity of arthropods in which insect blood (haemolymph) circulates.

Haemolymph Insect blood, usually colourless and clear, which fills the haemocoel.

Hemelytron (pl. hemelytra) Fore-wing of certain insects, e.g. triatomine bugs, which has a thickened basal part and a membranous distal part.

Hemimetabolous (incomplete metamorphosis) Describes the development from egg to adult which is gradual, passing through one or more nymphal stages, e.g. lice and ticks. If adults are winged the nymphal wing buds grow larger at each moult, e.g. bedbugs. There is no pupal stage. *See* Holometabolous.

Hereditary transmission Involves a female vector passing disease organisms to her eggs and thus to the next generation, i.e. transovarial transmission.

Hibernation Period of inactivity and/or altered behaviour caused by cold conditions, e.g. winter. Some mosquitoes, e.g. *Culex pipiens* in Europe, may remain in complete hibernation without blood-feeding for many months by living off their fat reserves. Other species, e.g. *Anopheles atroparvus*, enter incomplete hibernation, during which time adults need to emerge periodically from hibernation sites to take blood-meals to renew their fat reserves.

Holarctic Sometimes used to encompass the Palaearctic and Nearctic regions. *See* Zoogeographical regions.

Holometabolous (complete metamorphosis) Arthropod development from egg to adult in which the body form changes completely in appearance. A pupal or puparial stage is characteristic of holometabolous development. *See* Hemimetabolous.

Holoptic A condition of the head of adult Diptera in which the eyes meet or nearly meet each other, as, for example, in male adult simuliids. *See* Dichoptic.

Horizontal transmission Transfer of an infectious agent from one individual to another, excluding the process of transovarial and transstadial transmission. *See* Transovarial and Transstadial transmission.

Host preference Preferred hosts (e.g. species, sex, age) of an arthropod in an area when a choice exists. For a particular species this can alter from area to area as well as seasonally, depending usually on the availability of alternative hosts.

IGR *See* Insect growth regulator

Impoundment Well-defined man-made area of water, usually with more or less vertical sides, often constructed to provide water for domestic, agricultural or recreational puposes. However, impoundments are dug sometimes principally to reduce mosquito breeding in formerly marshy areas.

Infected Applied to arthropods when a parasitic infection has been taken up by the vector but is not yet in a stage in which it can be transmitted to a host. Examples are simuliid adults with onchocercal larvae in their flight muscles, or a vector with arboviruses in the stomach but not yet in the salivary glands. *See* Infective.

Infective Applied to arthropods when the parasites can be transmitted by the vector to a host. Examples are mosquitoes with malarial sporozoites in the salivary glands or simuliids with third-stage onchocercal worms in their mouthparts. *See* Infected.

Insect growth regulator (IGR) Sometimes known as insect development inhibitors, IGRs are groups of chemicals that either prevent the development of larvae into pupae or pupae into adults (juvenile hormone analogues, e.g. methoprene) or interfere with the moulting process, killing larvae as they moult (chitin synthesis inhibitors, e.g. diflubenzuron).

Insecticide resistance Ability of arthropods to tolerate doses of insecticide which would prove lethal to the majority of normal (susceptible) individuals of the same species. Rare mutants which are resistant are selected for by the use of the insecticide.

Instar One of a series of life-cycle stages in metamorphosis that are separated by a moult, e.g. the first, second and third larval instars of house flies and the five nymphal stages of bedbugs.

Integument The cellular epidermis and outer non-cellular cuticle which together provide the outer covering of arthropods. *See* Exoskeleton.

Intermediate host Host in which a parasite does not reach sexual maturity. Applies to most parasites in arthropod vectors, e.g. filarial parasites in mosquitoes and simuliids. *See* Definitive host.

Intrinsic incubation period Duration of the life cycle of a parasite in the vertebrate host; interval between infection and first clinical symptoms.

Karyotype The number and appearance of the chromosomes in the nuclei of a species.

Larviparous Reproduction in which the egg(s) hatch within the female and larva(e) are deposited, e.g. tsetse flies.

Life cycle (life history) In entomology and parasitology this usually means the series of morphological stages an organism passes through to reach the mature adult stage, and the biology of each stage.

Longevity How long an organism lives, often expressed as the mean expectancy of life. Vector longevity is one of the most important factors in disease transmission dynamics and vector control.

Maggot Legless larva that has no distinct head, thorax or abdomen, e.g. larvae of house flies.

Maintenance host A vertebrate or arthropod host which allows long-term survival of parasite populations. The host must have an infection rate that is at least adequate to maintain a population of the disease agent continuously endemic in an area. Humans can be maintenance hosts of louse-borne typhus, and mosquitoes and birds appear to be maintenance hosts of some of the encephalitis viruses. A maintenance host may retain an infection during periods when there is no or little vector transmission, e.g. during dry seasons or winters.

Mechanical transmission Transmission where there is no multiplication or cyclical development of the aetiological agent (i.e. parasite or pathogen), it being merely passively carried by the vector. Examples are house flies transmitting trachoma virus and dysenteries by their feet, vomit or faeces, and trypanosomes transmitted by stable flies (*Stomoxys* species).

Metacyclic trypanosome (metatrypanosome) The final, and usually smaller, version of the trypomastigote form in the vector that is infective for the vertebrate host.

Metamorphosis Changes in form from the first stage (egg) in the life cycle of an arthropod to the adult form. In hemimetabolous arthropods, e.g. bedbugs, lice, ticks and mites, the change is gradual through nymphal stages which resemble small versions of the adult. In holometabolous arthropods, e.g. mosquitoes, tsetse flies and fleas, the changes are abrupt and involve larval stage(s) and a pupal or puparial stage which are very dissimilar to the adult.

Microbial insecticide Insecticide comprising a biological agent such as bacteria, e.g. *Bacillus thuringiensis* var. *israelensis* and *B. sphaericus*, or toxic compounds derived from such agents.

Middle East Many definitions, but here covers land surrounding southern and eastern shores of the Mediterranean Sea, extending from Morocco to the Arabian Peninsula, including Egypt, Turkey, Iran, Iraq, Sudan and Libya.

Monolayer Thin film of a water-insoluble surfactant, e.g. isostearyl alcohols and lecithins, that have a very high spreading power on water. Mosquito larvae are unable to maintain normal contact with the water surface, and this combined with the reduction of dissolved oxygen content caused by monolayers causes their death.

Morphology The outward structure of an organism. Most arthropods are identified by their morphology, i.e. by their outer appearance.

Moulting (also spelt molting) Process of shedding the cuticle between developmental stages (i.e. instars).

Myiasis Invasion of vertebrate organs or tissues by larvae of Diptera that feed on living or dead tissues. Myiasis may be accidental, obligatory or facultative. Accidental myiasis usually involves people eating food contaminated with fly eggs or larvae; no real harm is caused; live larvae may be passed in excreta or vomit. Obligatory myiasis is when it is essential for fly larvae to live on a live host for at least part of their life; an example is the larva of the tumbu fly. In facultative myiasis fly larvae are normally free-living, often breeding in meat or carrion, but under certain conditions they may infect living hosts; examples are larvae of bluebottles and greenbottles infesting wounds. *See* Myiasis in the index for different forms of myiasis.

Natural organic insecticides Examples are pyrethrum and petroleum oils.

Nearctic region The USA, Canada, Greenland and northern Mexico. *See* Zoogeographical regions.

Neotropical region South America, Central America, southern Mexico and Caribbean islands. *See* Zoogeographical regions.

New World North, Central and South America, and the Caribbean area. *See* Old World.

Nicotinoids The nicotinoids such as imidacloprid and dinotefuran are a relatively new class of insecticides. They are related to nicotine, which has been used mainly as an agricultural insecticide. They act on the acetylcholine system, and are safe on mammals but kill a broad range of insect pests.

Nidicolous In medical entomology usually used to describe the habit of soft, and some hard, ticks of living in and around the homes, nests, burrows and caves of their hosts. Such ticks disperse little. *See* Non-nidicolous.

Nit Egg of a louse, such as a head louse.

Nocturnal Refers to activity during the night, such as blood-feeding in anophelines and appearance in vertebrate blood of nocturnally periodic microfilariae of some helminths, e.g. *Wuchereria bancrofti*.

Non-nidicolous Describes the habits of most hard ticks of living in open and exposed habitats away from their hosts' homes. Such ticks are often dispersed by mammals and birds over considerable distances. *See* Nidicolous.

Nymph In incomplete metamorphosis (hemimetabolous development) the stage in the life cycle that hatches from the egg (e.g. bedbugs, lice),

or the stage that arises through the moulting of the larval stage (e.g. ticks).

Old World All countries and areas east of the Americas. *See* New World.

Oocyst rate Percentage of mosquitoes that have malarial oocysts on the stomach.

Organochlorines (chlorinated hydrocarbons) Synthetic insecticides containing carbon, chlorine and hydrogen, e.g. DDT, dieldrin, HCH and methoxychlor.

Organophosphates Synthetic insecticides which are derivatives of phosphoric acid and hence all contain phosphorus, e.g. diazinon, dichlorvos and malathion.

Oriental region Asia east of Pakistan and south of the Himalayas and central China, covering Taiwan, Sri Lanka, and the Southeast Asia archipelago eastwards to include Sulawesi. *See* Zoogeographical regions.

Ornithophagic (ornithophilic) Arthropods that blood-feed on birds.

Osmoregulation The regulation of water balance in arthropods; maintaining the homeostasis (balance) of osmotic and ionic content of the body fluids.

Overwintering Describes the survival tactics of arthropods during winters. For instance adults (e.g. some mosquitoes) may cease feeding and ovipositing and enter a state of hibernation until warmer weather reappears and activity resumes. The growth and development of the immature stages (e.g. mosquito and simuliid larvae) may also slow down.

Palaearctic region Europe, North Africa, Asia north of the Himalayas and central China, Japan, Iceland, mid-Atlantic islands. *See* Zoogeographical regions.

Periodicity Several organisms, including both vectors and parasites, exhibit temporal periodicity in aspects of their behaviour. *See* Aperiodic, Diel periodicity, Diurnal, Nocturnal, Subperiodic.

Peritrophic membrane A thin tubular sheath secreted either by cells at the anterior end of the mid-gut (mosquito larvae, tsetse fly adults) or by cells lining the mid-gut (adult mosquitoes). It is found only in some insects. It supposedly forms a protective lining for the mid-gut, but its exact function remains largely unknown. In tsetse flies the peritrophic membrane plays a role in the cyclical development of human sleeping sickness trypanosomes.

Pheromone Chemical (semiochemical) released usually as an odour by an individual which produces reactions in others of the same species, e.g. sex pheromones in tsetse flies and ticks.

Phoresy Transport of an animal from one place to another by means of attachment to another animal, e.g. *Simulium neavei* larvae on freshwater crabs, and eggs of *Dermatobia* flies attached to adult female mosquitoes.

Polynesia A group of numerous islands in the west Pacific extending from Hawaii to New Zealand and including the Solomon Islands, New Caledonia, Fiji, Tuvatu, Tonga, Samoa, Cook Islands, Society Islands, and Tahiti.

Polytene chromosomes So-called giant chromosomes found only in certain tissues of Diptera, such as the ovarian nurse cells of half-gravid anophelines and larval salivary glands of simuliids. When stained they show distinct banding patterns which can often be used to identify species within species complexes. *See* Sibling species.

Promastigote (leptomonad) Morphological form of a trypanosomatid with the flagellum arising near the anterior end, e.g. *Leishmania* parasites in the phlebotomine sand fly gut.

Pseudopod (false leg) Stumpy protuberances present on dipterous larvae of some species (e.g. tabanids, phlebotomine sand flies) that assist them in locomotion. None of the larvae of the Diptera possesses true legs.

Pseudotracheae Small tubes in the labella of the adults of some Diptera (e.g. muscids, calliphorids and tabanids) which are supported by sclerotized rings. Liquid food passes through minute openings in these pseudotracheae to the mouth of the fly.

Puparium Life-stage resulting from the hardening and sclerotization of the cuticle of the last larval instar of certain Diptera, e.g. tsetse flies and house flies. Equivalent to the pupa of other insects.

Pyrethroids A large group of synthetic insecticides structured to be similar to natural pyrethrum but which are more effective. Examples are permethrin, deltamethrin, and cypermethrin.

Questing The behaviour of ticks, mainly ixodids, when climbing up vegetation, such as grasses and herbaceous plants, in order to actively seek out passing hosts, to which they attach themselves.

Quiescence Temporary state of arrested or slowed development, such as in ixodid larvae after blood-feeding but prior to moulting to the nymphal stage, or state of inactivity of some hibernating adult mosquitoes.

Reservoir host An animal in which populations of disease organisms persist indefinitely, and which passes the disease to other species of hosts, often by vectors. Reservoir hosts may be maintenance hosts, and are often mammals and birds. Some arthropod vectors which are long-lived, and may also be capable of transovarial transmission, are sometimes regarded as reservoir hosts, e.g. ticks as vectors of relapsing fever and various viruses.

Residual spraying Application of a persistent insecticide (e.g. malathion) to surfaces such as to the inside walls and roofs of houses in malaria control programmes, and to trees in tsetse control projects.

Rickettsiae A group of Gram-negative intracellular coccoid-shaped bacteria, many of which are transmitted by arthropods, e.g. *Rickettsia prowazekii* transmitted by body lice and causing typhus. Formerly

rickettsiae were regarded as microorganisms intermediate between bacteria and viruses.

Sclerotization Process which results in the new arthropod cuticle formed after moulting being tanned (darkened) and hardened to give it rigidity.

Seed tick Name often given to the very small larva of an ixodid tick before it has blood-fed.

Sex pheromone A chemical compound produced by a species that attracts members of the opposite sex of the same species. Such chemicals can be used to lure species to traps so that they can be killed.

Sibling species (isomorphic or cryptic species) Species that are morphologically indistinguishable or almost so, and which are recognized by non-morphological features, usually their polytene chromosomes (e.g. species of the *Simulium damnosum* complex). In nature they are reproductively isolated from each other. Sibling species may differ only slightly biologically but be significantly different in epidemiological importance.

s. l. (sensu lato) Means in the broad sense. When placed after the name of a species denotes that reference is made not just to that species but also to closely related species (e.g. sibling species) within a complex. *See* s. str.

Source reduction Simple measures that either prevent breeding of arthropods or eliminate their breeding sites. Mainly applicable to mosquito control, e.g. covering water tanks, filling in puddles or removing discarded water-retaining receptacles.

Species A group of individuals in natural populations that can interbreed by mating within the group and producing fertile progeny; individuals are usually similar in appearance and behaviour.

Species complex A group of sibling, or very closely related, species that are morphologically indistinguishable (isomorphic) but are reproductively isolated, and which often live in the same area (sympatric). Species within a complex can often be identified by their polytene chromosomes or by biochemical or molecular techniques. The Diptera contain many complexes, such as in mosquitoes (e.g. *Anopheles gambiae* complex) and simuliids (e.g. *Simulium damnosum* complex).

Species group Used for an assemblage of closely related species that although they may be morphologically similar in one or more life-stages can nevertheless be distinguished on external appearance as distinct species, e.g. the *Simulium neavei* group – comprising eight species including *S. neavei*, *S. woodi* and *S. nyasalandicum*.

Species sanitation Control, or eradication, directed against just one species of vector or pest in a particular area, usually using simple techniques.

Spermatheca One or more receptacles in the female reproductive system of arthropods which receive sperm during mating.

Spirochaetes Gram-negative bacteria which have a more or less spiral shape, e.g. *Borrelia duttonii*, which is spread by soft ticks and causes relapsing fever.

Sporogony That part of the sexual cycle of sporozoans (e.g. *Plasmodium* species) in which sporozoites are produced.

Sporozoite rate Percentage of mosquitoes with malarial sporozoites in their salivary glands.

s. str. (sensu stricto) Means in the strict, or narrow, sense. When placed after a species name denotes that only that species is being referred to, and not any of its closely related (e.g. sibling) species in a complex. Sometimes abbreviated to s. s. *See* s. l.

Sterile male release (sterile-insect technique, SIT) In genetic control programmes the inundative release of large numbers of artificially sterilized male arthropods into field populations in the hope that this will result in sterile matings and consequently a reduction in population size.

Subperiodic As applied to microfilariae in peripheral vertebrate blood, means they exhibit partial diel (24-hour) periodicity. That is, their concentration in the blood decreases from a maximum to a minimum, but not close to zero as with microfilariae showing periodic periodicity. Diurnal subperiodicity occurs in the Pacific strain of *Wuchereria bancrofti*, while nocturnal subperiodicity is found in populations of *Brugia malayi* in West Malaysia, Thailand, etc.

Subspecies In zoology the only taxon recognized below the rank of species. Subspecies differ morphologically from other members of the species and are spatially isolated, e.g. either geographically or by their hosts. Consequently they are normally reproductively isolated, but when brought together can interbreed with other subspecies. Subspecies may eventually evolve into distinct species.

Sylvatic In epidemiology means that diseases are contracted in woods or forests, e.g. the forest cycle of yellow fever. *See* Campestral.

Sympatric Two or more species that occur in the same geographical areas. See Allopatric.

Synanthropic Applied to animals living in close association with humans or their houses, e.g. house flies and triatomine bugs.

Synergist Chemical that has little or no toxicity but, when combined with some insecticides, enhances their activity and thus reduces dosage rates. For example, piperonyl butoxide is a synergist added to the insecticide pyrethrum.

Transovarial transmission Production by an infected vector of eggs infected with parasites (e.g. viruses, rickettsiae). When they hatch they give rise to individuals (e.g. larvae, nymphs) that are infected and are either capable of transmitting the parasites (e.g. ticks) or passing it on to later life-cycle stages that transmit the infection (e.g. scrub typhus mites). *See* Hereditary transmission.

Transstadial transmission Survival of parasites through successive life-cycle stages (larva → nymph(s) → adult) of an organism (e.g. ticks), each of which can transmit the parasite if it is haematophagous.

Trypomastigote Morphological form of a trypanosome with the flagellum arising near the posterior end, and running the length of the body

where it is attached to the cell membrane. Trypomastigotes are found in the vertebrate blood of hosts infected with trypanosomiasis, and are the form ingested by a vector with its blood-meal.

Ultra-low-volume (ULV) Refers to spraying an insecticide in concentrated form; thus the dosage rate is small, e.g. 5 litres/hectare.

Vector Organism that conveys an aetiological agent from one host to another. A vector may be an intermediate host (e.g. culicines transmitting filariasis) or not (e.g. house flies mechanically transmitting bacteria).

Venereal transmission When pathogens, such as viruses and rickettsia, are passed from congenitally infected males to females during mating, Occurs in some vectors of yellow fever and Crimean–Congo haemorrhagic fever.

Vertical transmission This refers to the transfer of a pathogen from a parent to its offspring, such as by transovarial and transstadial transmission. *See* Transovarial and Transstadial transmission.

Viraemia Presence of virus in vertebrate blood. High viraemias are usually necessary for transmission by arthropod vectors.

Wettable powder (water-dispersible powder) Technical grade insecticide diluted with an inert carrier (dust) and to which a wetting agent or surfactant has been added. The resultant wettable powder is then mixed with water for spraying onto surfaces.

Zoogeographical regions Any one of the six main geographical areas referred to by zoologists. Each region has its own particular fauna, of which many species occur only in that region. The Palaearctic and Nearctic regions are sometimes grouped together and referred to as the Holarctic region. *See* Afrotropical, Australasian, Nearctic, Neotropical, Oriental and Palaearctic regions.

Zoonosis An infection that is naturally transmitted between vertebrate hosts and humans.

Zoophagic (zoophilic) Blood-sucking arthropods that feed on non-human animals

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